Part 4

The Nuts and Bolts of Invasion Ecology

Chapter 9

A MOVEMENT ECOLOGY APPROACH TO STUDY SEED DISPERSAL AND PLANT INVASION: AN OVERVIEW AND APPLICATION OF SEED DISPERSAL BY FRUIT BATS

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9.1 BIOLOGICAL INVASIONS AND DISPERSAL PROCESSES

Biological invasions – the entry, establishment and spread of non-native species – are a major cause of human-induced environmental change (Vitousek et al. 1997; Ricciardi 2007). Beyond their substantial economic impact and human health hazards (Vitousek et al. 1997; Pimentel et al. 2001), biological invasions threaten global biodiversity by altering the structure and function of ecosystems and disrupting key biological interactions (Levine et al. 2003; Traveset & Richardson 2006). Consequently, they also constitute a major cause of recent extinctions (Clavero & García-Berthou 2005; but see Didham et al. 2005).

Dispersal, or the unidirectional movement of an organism away from its home or place of birth, is a key process in an organism's life cycle, operating at multiple scales and levels of organization from the single organism through population, metapopulation and community dynamics (Harper 1977; Clobert et al. 2001; Bullock et al. 2002; Cousens et al. 2008; Nathan et al. 2009). For many plants seed dispersal is the primary mobile stage, typically mediated by vectors that disperse seeds over short distances, affecting local-scale plant population and community persistence, structure and dynamics (for recent reviews, see Cousens et al. 2008, Nathan et al. 2009 and references therein). Relatively few seeds are dispersed over long distances (long-distance dispersal (LDD)), affecting large, landscape-scale dynamics of plant populations and communities (Nathan 2006). Defining which dispersal events account for LDD typically involves setting arbitrary or system-specific thresholds, taking either a proportional approach (e.g. all the seeds that travelled the upper 1% of the distance distribution) or an absolute approach (e.g. all the seeds that travelled more than 1000 m, as adopted in section 9.4 of this chapter); the latter is generally preferable, mostly for practical reasons (see Nathan et al. 2008b for discussion).

The vector-mediated seed dispersal process consists of three main phases, each characterized by a basic, key parameter (Nathan et al. 2008b; Table 9.1): (i) the initiation phase, in which seeds are picked up by the vector, characterized by the vector's 'seed load' parameter, or the number of seeds taken per time unit; (ii) the transport phase, in which the vector transports the seeds away from the source, characterized by the vector's 'displacement velocity' parameter after seed uptake; and (iii) the termination phase, in which the seeds are deposited, characterized by the vector's 'seed passage time' parameter, or the duration of seed transport by the vector. The contribution of different vectors to local dispersal versus LDD depends mostly on the two former parameters (Nathan et al. 2008b). LDD vectors, for example, should at least occasionally have high displacement velocity, and are especially efficient when combined with long seed passage time (Nathan et al. 2008b; Schurr et al. 2009). Human transportation is presumably the only mechanism which has a high relative effect on all three parameters, making mankind the most important LDD vector nowadays.

In 1958 Charles Elton launched the systematic scientific study of biological invasions with the publication of his book *The Ecology of Invasions by Animals and Plants* (Elton 1958; reviewed in Richardson & Pyšek 2008). Though Elton argued that the major cause for spread of species was the increased extent of human travel around the globe, he noted that even without human intervention, 'exceptionally good powers of dispersal' (Elton 1958, p. 33) have enabled many species to spread and achieve a wide distribution, hence acknowledging the importance of LDD for the dynamics of population spread. It is the arrival of humans, Elton wrote, that has made 'this process of dispersal so much easier and faster' (Elton 1958, p. 79). Dispersal is now recognized as a major and essential component in the dynamics of invasions (see also Hui et al., this volume). However, although dispersal is necessary it is insufficient to generate continuing spatial spread: dispersed seeds must germinate, survive and grow to become reproductive plants that produce and disperse seeds, and so forth. Thus plant dispersal occurs within one generation (usually lasting a very short time), whereas continuing spread is a multi-generation process.

The process of biological invasion can generally be divided into three dynamic stages – entry, establishment and spread – with barriers, or filters, hindering or preventing transition from one stage to the next (Richardson et al. 2000b; Colautti & MacIsaac 2004). Although dispersal is not the only filter plants must pass through, it is an important one that has key impacts on the survival and success of the invading plant. The entry stage often results from human-mediated extreme LDD (Mack & Lonsdale 2001; Ricciardi 2007; Hulme et al. 2008), but might also result from other LDD mechanisms if the invading species is already present as an alien in a neighbouring region (Hulme et al. 2008). Natural dispersal by man-

made infrastructures connecting otherwise unlinked biogeographical regions (e.g. Lessepsian migration through the Suez Canal (Por 1978; Ben-Eliahu & ten Hove 1992)) may also bring about the initial introduction of alien species (Hulme et al. 2008). The establishment stage involves mainly local dispersal, whereas the spread stage involves rapid expansion that is mostly dominated by LDD (Kot et al. 1996; Clark 1998). In these two post-entry stages, humans play an increasingly important role (see, for example, Von der Lippe & Kowarik 2007), yet natural vectors are probably still the key dispersers (Debussche & Isenmann 1990; Richardson et al. 2000a; Murphy et al. 2008; Westcott et al. 2008). Dispersal at the post-entry stage is crucially important to the extent that successful dispersal away from the initial point of introduction marks the transition from 'alien' through 'naturalized' to 'invasive' (*sensu* Richardson et al. 2000b). Therefore, dispersal is a necessary step at several stages of the plant's invasion; understanding dispersal processes not only to, but also within, the invaded region is therefore crucial for understanding and predicting invasion success (Richardson et al. 2000a; Higgins et al. 2003a; Buckley et al. 2006).

The aims of this chapter are to review the progress in seed dispersal research especially in the context of plant invasion (section 9.2), and to introduce (section 9.3) and illustrate (section 9.4) a general framework for elucidating the role of dispersal mechanisms as a major driving force in invasion processes.

9.2 OVERVIEW OF THE CONCEPTS AND METHODS APPLIED TO QUANTIFY SEED DISPERSAL PATTERNS AND UNDERSTAND THEIR UNDERLYING MECHANISMS

Advances in understanding dispersal

Research during the past 50 years has yielded innovative insights into the ecological and evolutionary processes underlying dispersal in general (Bullock et al. 2006; Nathan et al. 2009) with recent advances in LDD in particular (Cain et al. 2000; Nathan 2006; Nathan et al. 2008b). Seed dispersal research has seen an important shift in focus in recent years, from the traditional 'seed-centred' approach focusing on seed attributes and asking by which mechanisms and over which distances these seeds are dispersed, to a 'vector-

centred' approach now focusing on a dispersal vector and asking how many seeds this vector disperses over which distances (Nathan et al. 2008b; Schurr et al. 2009).

Studies have shown that 'standard' vectors, those inferred directly from seed morphology, have low impact on LDD and spread rate, compared with other, 'non-standard' vectors (Higgins et al. 2003b; see examples in Nathan et al. 2008b). Nevertheless, and despite the common consensus that LDD events are rare and largely unpredictable under most circumstances, LDD is strongly associated with a limited and identifiable set of environmental conditions and dispersal vectors (Nathan et al. 2008b). Six major generalizations of mechanisms that likely promote plant LDD have been identified (Nathan et al. 2008b), such as open terrestrial landscapes that are free of obstacles to seed and vector movement and thus have a relatively long seed passage time; migratory animals that move in a fast and directional manner and thus have a relatively high displacement velocity; extreme meteorological events that can result in exceptionally high displacement velocity and seed load; and human transportation, presumably the mechanism most likely to move seeds the longest possible distances (Nathan et al. 2008b).

A parallel, highly relevant shift in seed dispersal research has been the relatively recent recognition that animal seed dispersers tend to be generalists rather than specialists (Richardson et al. 2000a; Herrera 2002) and that the coevolutionary vector–seed interactions are not as tight and common as was previously thought (Richardson et al. 2000a; Bascompte et al. 2006). Overall, dispersal systems are complex assemblages of multiple dispersers operating at various scales to generate jointly the 'total dispersal kernel' (Nathan et al. 2008b). Therefore, taking the vector-based approach of seed dispersal in investigating invasion processes requires identifying the key players facilitating passage through the dispersal-related invasion filters, such as in the initial introduction stage (Hulme et al. 2008).

Advances in data collection

Tracking seed movement away from the source plant has always been a challenging, and often limiting, part of studying seed dispersal patterns and mechanisms (Wheelwright & Orians 1982; Nathan &

Muller-Landau 2000; Wang & Smith 2002). This has been especially true when attempting to quantify and identify LDD processes in the field (Cain et al. 2000; Nathan 2006). Seed traps have made an important contribution to dispersal research (see, for example, Clark et al. 1998, Bullock & Clarke 2000) and are still being used today, despite several inherent problems given the difficulty in identifying the source of the seeds (Nathan & Muller-Landau 2000), though this can be resolved using genetic methods (see, for example, Jones et al. 2005). Artificially marking seeds at the source and finding their deposition sites (Levey & Sargent 2000; Xiao et al. 2006) has become increasingly used, and novel methods are still being developed (Carlo et al. 2009; Lemke et al. 2009). Controlled manual seed release is also advancing current wind dispersal research (Tackenberg 2003; Soons et al. 2004).

Research on animal-dispersed plants has progressed from directly observing animal movement, to tracking the animals with radio-telemetry (see, for example, Murray 1988; Westcott & Graham 2000; Spiegel & Nathan 2007). Recent technological advancements such as satellite-tracking using the Argos system or tracking units based on global positioning systems (GPS) have revolutionized the quality, quantity and scale of animal tracking data in the wild; this, in turn, also improved the input parameters inserted into models predicting the animal's seed dispersal ability (Campos-Arceiz et al. 2008). However, two main drawbacks – high costs and heavy power supply – currently limit their use and make most small-sized animals unapproachable by such technologies. Future miniaturization will enable tracking of many additional animal vectors and even seeds at large scales with the high spatio-temporal resolution required to revolutionize this field of research.

The study of genetic variation and molecular ecology has seen tremendous technological and analytical advancements in the past few decades (Ouborg et al. 1999; Cain et al. 2000; Jones & Ardren 2003). This has provided extremely useful data collection and novel analysis methods, that have enabled us to track relatedness of individual seeds and their dispersing plant (Godoy & Jordano 2001; Jones et al. 2005; Jordano et al. 2007; Robledo-Arnuncio & García 2007) or relatedness of individual plants and their dispersing parent (i.e. effective seed dispersal) (Meagher & Thompson 1987; Burczyk et al. 2006; González-Martínez et al. 2006; Hardesty et al. 2006). Valuable inferences on historical gene flow can also be gained by using molecular methods, revealing important ecological and evolutionary consequences of dispersal (Cain et al. 2000; Broquet & Petit 2009).

Advances in modelling and statistical analysis

Models of seed dispersal have played a fundamental role in representing patterns, investigating processes, elucidating the consequences of dispersal, and explaining dispersal evolution for populations and communities (Levin et al. 2003). In addition, modelling is often applied to predict dispersal rates, directions and intensity, which is of prime importance in assessing invasion dynamics (Higgins & Richardson 1999; Neubert & Caswell 2000; Higgins et al. 2003a; Skarpaas & Shea 2007; Jongejans et al. 2008; Soons & Bullock 2008). Modelling studies elucidating the potential role of spatial heterogeneity in determining invasion speed (With 2002) facilitated the development of models predicting dispersal in a spatially explicit and realistic environment (Russo et al. 2006; Levey et al. 2008; Schurr et al. 2008).

A common goal in modelling seed dispersal is estimating the dispersal kernel, the probability density function describing the number (or density) of dispersal units as a function of the distance from the source. In general, we can distinguish between two types of models for seed dispersal: phenomenological and mechanistic (Nathan & Muller-Landau 2000). Phenomenological models have been frequently used to estimate dispersal kernels for plant species (Kot et al. 1996; Clark 1998; Higgins & Richardson 1999; Bullock & Clarke 2000). These models use some functional forms, calibrated against observed data, to describe the distribution of distances of progeny from the seed source. Because model parameters are fitted from observed data, the identity of the dispersal agents is unimportant, thus relaxing the need to identify and quantify the role of different dispersal vectors. Phenomenological models enable us to deduce the spread potential of the plant simply by analysing the kernel tail 'fatness', which largely determines the speed and pattern of colonization (Kot et al. 1996; Clark 1998; Clark et al. 1998; Higgins & Richardson 1999; Higgins et al. 2003a; reviewed in Klein et al. 2006). However, this approach entails several disadvantages, including the high sensitivity of the fitted functions to variation not only in dispersal data but also in data

Table 9.1 Specific parameters of the three key components of a general model for passive dispersal (Nathan et al. 2008b) for four major dispersal systems.

	Anemochory	**Hydrochory**	**Endozoochory**	**Epizoochory**
Vector seed load (seeds time⁻¹)	Seed abscission rate (potentially wind-induced)	Seed abscission rate (potentially wind- or water-induced)	Seed intake rate	Seed adhesion rate
Displacement velocity (distance time⁻¹)	Flow speed		Animal movement speed	
Seed passage time (time)	Seed release height divided by seed terminal velocity	Seed buoyancy time	Gut retention time	Adhesion time

collection procedures (Hastings et al. 2005). The variation in dispersal processes between species, sites and times implies that this modelling approach is best used for a posteriori analysis of invasions (Higgins & Richardson 1999), which can also be achieved by models that correlate the observed patterns of spatial spread of invasive species with climatic, edaphic or other environmental variables (Peterson & Vieglais 2001; Foxcroft et al. 2004).

Compared with phenomenological models that calibrate dispersal kernels, mechanistic models use data on factors influencing dispersal processes to predict dispersal kernels. The general model for vector-mediated dispersal (Table 9.1) disentangles three basic components, from which further modelling can be carried out on specific cases of vectors and systems. A great deal of work in mechanistic modelling of seed dispersal by wind has been done since the publication of Elton's book, especially in recent years (Okubo & Levin 1989; Nathan et al. 2002; Tackenberg 2003; Soons et al. 2004; Bohrer et al. 2008; Wright et al. 2008; reviewed in Kuparinen 2006). An important advance has been made in fitting mechanistic models to LDD by wind, which earlier models often underestimated and could not explain (Nathan et al. 2002; Tackenberg 2003). Recent studies have shown that wind-speed-induced non-random seed release promotes LDD and increases spread rates (Soons & Bullock 2008), and that canopy structure height affects vertical winds and turbulence structure which in turn affect LDD (Bohrer et al. 2008). Mechanistic models of seed dispersal by animals, in their simplest form, calculate dispersal distances as the product of the vector seed load, displacement velocity and seed passage time (Table 9.1; Murray 1988; Sun et al. 1997; Holbrook &

Smith 2000; Westcott & Graham 2000; Vellend et al. 2003; Wehncke et al. 2003). These models are amenable for incorporating the effects of dispersal by multiple vectors (Dennis & Westcott 2007; Spiegel & Nathan 2007), including 'non-standard' vectors such as cassowaries dispersing the invasive 'water-dispersed' pond apple (Westcott et al. 2008).

9.3 SEED DISPERSAL AND MOVEMENT ECOLOGY OF INVASIVE SPECIES

Seed dispersal research can have important contributions to the field of plant invasion. By applying methodologies developed for seed dispersal research, researchers may improve their understanding of the relationships between invasive plants and their vectors, and better understand the dynamics of species spread within the landscape. Seed dispersal can be generalized within the movement ecology framework, enabling researchers from different disciplines to standardize the study of seed dispersal processes, and to identify the key life history traits, behaviours and external factors determining seed movement (Nathan et al. 2008a).

Movement ecology mechanistically defines the movement of organisms by four basic components and their interaction: internal state (why move?), motion capacity (how to move?), navigation capacity (where and when to move?) and external factors influencing all of the above (Nathan et al. 2008a). Although plants differ considerably from animals in their movement ability, their spatial movement can be conveniently implemented within the movement ecology framework. The external factors of the plant movement

ecology framework are proximate extrinsic drivers determined at ecological time spans (Damschen et al. 2008; Nathan et al. 2008a), including environmental characteristics in general and the dispersal vectors in particular. The internal state, motion capacity and navigation capacity are plant attributes selected by ultimate drivers operating mostly at evolutionary time spans (Damschen et al. 2008; Nathan et al. 2008a). In the evolutionary sense, the internal drivers of dispersal, as identified in basic dispersal theory, include bet-hedging in unpredictable ecological conditions, avoiding kin competition and distance- or density-dependent mortality, and promoting outbreeding (Howe & Smallwood 1982; Levin et al. 2003; Nathan et al. 2009). Motion capacity, defined as the traits enabling seed movement, includes plant, fruit and seed characteristics that facilitate transport by external vectors such as plant height, fruit colour and scent, seed size and shape, and fruit and seed structural and chemical composition (Jordano 2000; Herrera 2002). The navigation capacity of plants primarily refers to the traits that synchronize the timing of fruiting and seed release with favourable dispersal conditions (Wright et al. 2008).

Mechanistic models for seed dispersal by wind effectively fit into this conceptual framework, incorporating atmospheric conditions (external factors) and plant traits such as wings and hairs enabling transport by wind (motion capacity) and seed abscission tissue determining timing of seed release (navigation capacity) as input parameters, outputting seed dispersal trajectories (movement); these, in turn, enable predictions of post-dispersal patterns to assess potential consequences for fitness (internal state), such as the probability of hitting a non-occupied establishment site away from sibling seeds (Wright et al. 2008).
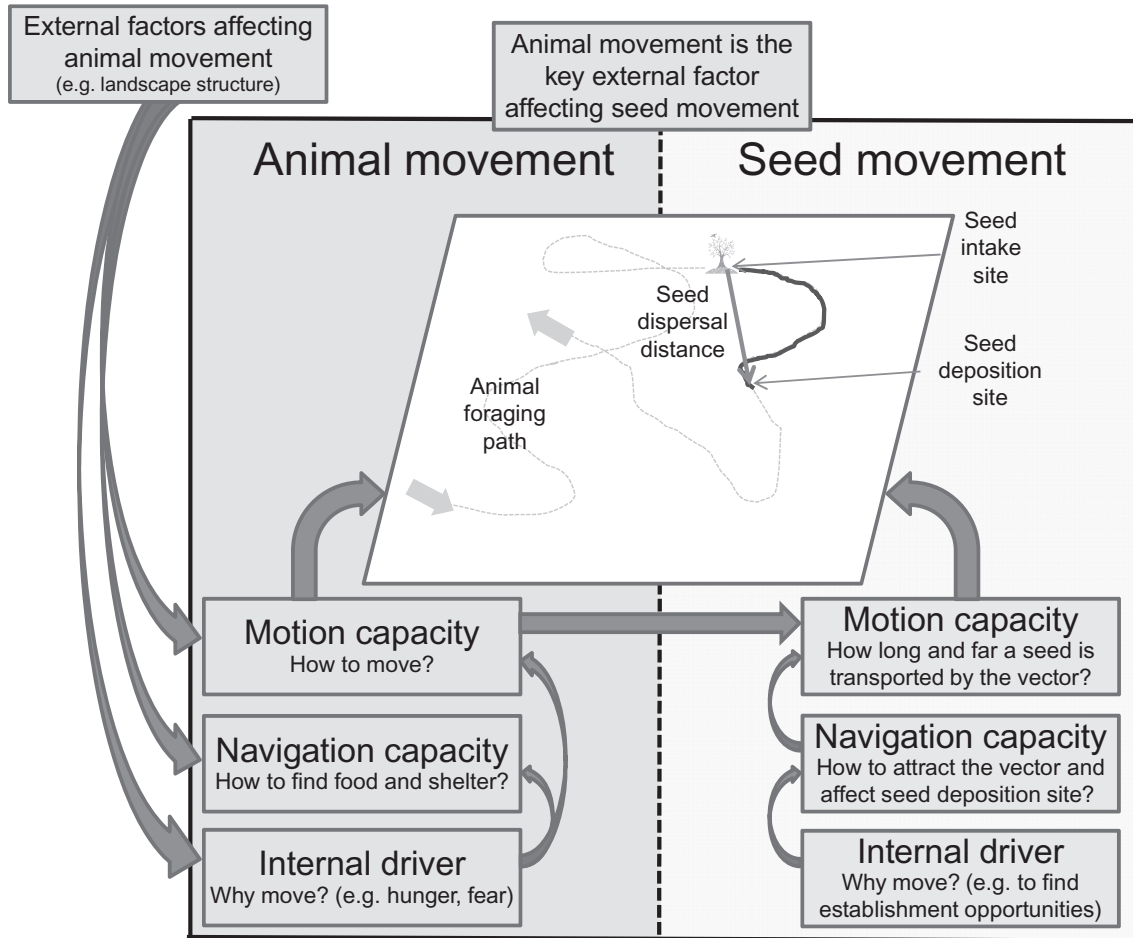
Applying the movement ecology framework to the movement of animal-dispersed plants necessitates a twofold nested design (Fig. 9.1). In the inner loop, the dispersed seed is the focal individual and the vector is a major external factor affecting its movement. In the outer loop, the animal serving as the dispersal vector is the focal individual. In other words, modelling seed dispersal by animals requires considering not only the movement ecology of the plant but also the movement ecology of its vectors. The interplay between the two will ultimately determine the movement path of the plant. From the animal disperser's point of view, the internal state includes the need to obtain food (the properties of which are determined by the plant), to

avoid predators, to seek shelter, etc. The motion capacity relates to the internal machineries enabling animals to fly, walk, swim, climb, etc. The navigation capacity comprises the animal's ability to sense and respond to environmental cues related to movement by using, for example, the visual, olfactory or auditory systems, echolocation and magnetic field detection. Among the many biotic and abiotic external factors affecting these three internal components of animal movement are landscape structure, atmospheric or meteorological conditions, movement of predators and location or movement of food sources (Nathan et al. 2008a).

Identifying the relevant crossroads of interactions between the plant and the vector is where the movement ecology framework can greatly assist in identifying traits and mechanisms that could, at least partly, explain and predict plant dispersal processes. Fruit and seed characteristics interact with the set of frugivores the plant attracts, which in turn may differ in their navigation and motion capacities resulting in different movement paths of the seeds. For example, synchronization of fruiting with the passage of long-distance migrating animals could favour LDD and population spread, whereas attracting dispersers that consume fruit and rest on the source plant would favour dispersal over shorter distances. This also depends on the seed passage time and for some animals on the timing of fruiting (e.g. during the breeding season animals may carry seeds back to their offspring or mate).

In the following part we will apply movement ecology to examine the potential of a flying frugivore to disperse seeds of native and potentially invasive species. Studies of plant–vector interactions of an invasive species need not wait until empirical data on the invasion process itself becomes available, but can reasonably assume that, at least in early stages of invasions, animal movements are not significantly affected by the presence and distribution of the invading plant itself (Richardson et al. 2000a). This can be explained by the fact that at early stages the invading plant species is relatively rare and unfamiliar to the foraging animal. Thus, *a priori* predictions of the spread of potentially invasive animal-dispersed plants can be based on existing data on the foraging movements of local animal species capable of serving as dispersal vectors. Furthermore, comparing the properties of the different framework components between sympatric native and alien plants, or a potentially invasive plant in its native versus invaded range, could facilitate understanding of invasion dynamics and success, and

Fig. 9.1 A general conceptual framework for movement ecology of animal-dispersed plants. The framework has a twofold nested design (see main text). In the inner loop, the dispersed seed is the focal individual and the animal (the dispersal vector) is the major external factor affecting its movement. In the outer loop, the dispersal vector is the focal individual.

could assist in identifying invasion filters and pointing out candidate elements for management plans (Buckley et al. 2006).

### 9.4   FRUIT BATS AS LONG-DISTANCE SEED DISPERSERS OF BOTH NATIVE AND ALIEN SPECIES

Our illustration of the movement ecology approach focuses on seed dispersal of native and alien (including naturalized and potentially invasive) plant species (*sensu* Richardson et al. 2000a) by a common generalist dispersal vector, the Egyptian fruit bat (*Rousettus aegyptiacus*). We apply the twofold nested design of movement ecology (Fig. 9.1) to predict bat-mediated dispersal of the two groups of species, combining vector movement, foraging behaviour and seed passage time. In addition to this specific case study, we will show how simple allometric relationships can predict the seed dispersal distance for frugivorous birds and mammals (Box 9.1).

Box 9.1 Allometric relationships as a generic model for animal seed dispersal

Allometric relationships between body mass and various other characteristics of organisms have been well studied (Calder 1996). Animals with a larger body mass are predicted to have a larger home range, higher travel velocity and longer seed retention time, compared with smaller animals within the same taxonomic

(a)

(b)
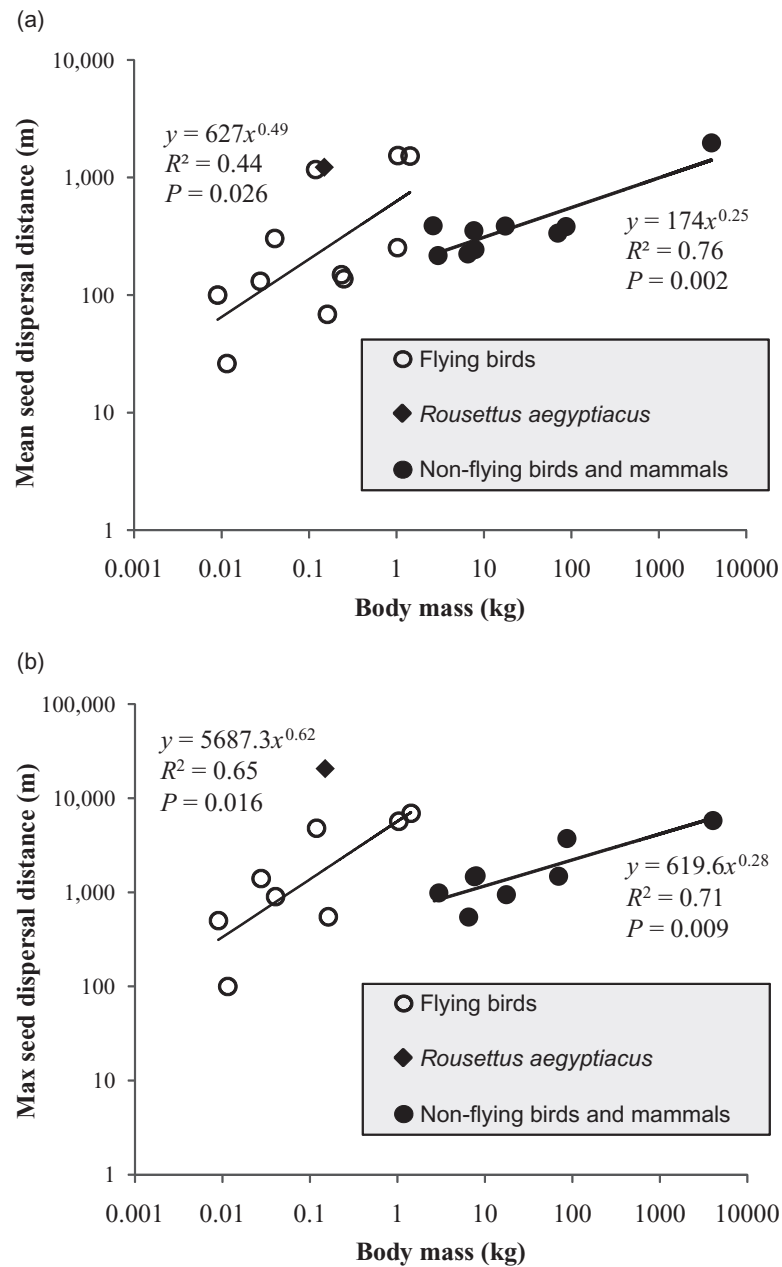
group (Calder 1996). Larger animals are therefore expected, by allometric relations alone, to disperse seeds to greater distances (Westcott & Graham 2000). Moreover, large animals often take up seeds of a wide variety of plant species, irrespective of the plant's dispersal morphology (see, for example, Westcott et al. 2005). Schurr et al. (2009) presented a meta-analysis of endozoochorous dispersal by birds, showing that seed dispersal distance increases with the body mass of avian dispersers as predicted from allometric relationships. They presented a simple general model that relates the body mass of animals to the mean dispersal distance of the seeds they disperse endozoochorously. Here we tested Schurr's et al. (2009) prediction with additional data, as well as with our own data of the Egyptian fruit bat (see section 9.4), and compared it with allometric predictions for flying birds, mammals and non-flying birds (see Rowell & Mitchell 1991; Mack 1995; Zhang & Wang 1995; Julliot 1996; Sun & Moermond 1997; Sun et al. 1997; Holbrook & Smith 2000; Stevenson 2000; Westcott & Graham 2000; Mack & Druliner 2003; Vellend et al. 2003; Wehncke et al. 2003; Westcott et al. 2005; Russo et al. 2006; Pons & Pausas 2007; Spiegel & Nathan 2007; Ward & Paton 2007; Weir & Corlett 2007; Campos-Arceiz et al. 2008).

Mean gut retention time (GRT) and mean speed of movement (SM) can both be expressed allometrically as a function of animal body mass (BM) (Robbins 1993; Calder 1996). For birds, these relationships were estimated as

$$GRT(h) = 1.6 BM_{(kg)}^{0.33} \quad \text{(Robbins 1993)} \tag{1}$$

and

$$SM(m/s) = 15.7 BM_{(kg)}^{0.17} \quad \text{(Calder 1996)} \tag{2}$$

For the Egyptian fruit bat's mean body mass measured in our study (147.5 ± 11.1 g), mean GRT from equation (1) is 51.1 minutes, very close to our measured value (52.82 ± 26.5 minutes). The mean SM from equation (2) is 11.34 m/s, higher than our measured value (9.1 ± 0.86 m/s). Indeed, owing to their general wing shape and flight mode, bats are expected to fly more slowly than birds of similar mass (Hedenström et al. 2009). Theoretical modelling of Egyptian fruit bat power flight (Flight 1.21 software (Pennycuick 2008)) predicts a minimum power speed of 9.3 m/s, in agreement with our empirical results.

We fitted a power curve to literature data of mean and maximum dispersal distances against mean disperser body mass, and compared it with our own predictions of the Egyptian fruit bat's dispersal kernel (Box Fig. 1). The mean and maximum seed dispersal distances by the Egyptian fruit bat are obviously much larger than expected for non-flying birds and mammals, and fairly similar to those of flying birds, though higher than expected, implying the large contribution fruit bats may have for LDD. In general, this multi-species analysis provides the means to approximate the dispersal potential of different vectors from body mass alone, or serve as a generic model for the expected dispersal distances of species differing in their body mass.

Box Fig. 1 The allometric relationships between body mass and the mean (a) and maximum (b) dispersal distances, divided into flying birds (*Onychognathus tristramii*, *Pycnonotus xanthopygos*, *Mionectes oleagineus*, *Ceratogymna atrata*, *Ceratogymna cylindricus*, *Dicaeum hirundinaceum*, *Garrulus glandarius*, *Pycnonotus jocosus*, *Corythaeola cristata*, *Tauraco schuetti* and *Ruwenzorornis johnstoni*) and non-flying birds and mammals (*Casuarius bennetti*, *Casuarius casuarius*, *Odocoileus virginianus*, *Cebus capucinus*, *Ateles paniscus*, *Lagothrix lagotricha*, *Alouatta seniculus*, *Cebus apella* and *Elephas maximus*). The figure includes data presented in this chapter for *Rousettus aegyptiacus*.

Most fruit bats of the Pteropodidae family are generalist consumers of a high variety of fruit species (Marshall 1983; Muscarella & Fleming 2007). They are common within the Old World tropical region and are claimed to be one of the major seed dispersers of tropical ecosystems (Mickleburgh et al. 1992), yet have been studied mainly for the type of fruit they consume and their qualitative potential contribution to dispersal (see, for example, Shilton et al. 1999; Muscarella & Fleming 2007; Nakamoto et al. 2009).

One of the most widely distributed bats within the Pteropodidae family is the Egyptian fruit bat (*Rousettus aegyptiacus*), a medium sized bat (100–200 g) that is considered a generalist forager, feeding on almost all fleshy fruited trees within its range including native, alien, naturalized and invasive species (Izhaki et al.

1995; Korine et al. 1999; Kwiecinski & Griffiths 1999). The Egyptian fruit bat exhibits commensalism with humans, commonly foraging in rural and urban habitats (Korine et al. 1999). Thus, as a human commensal and generalist feeder, the species has a large potential to disperse alien plants at the post-entry stage and in areas neighbouring human-dominated environments, where it has a higher probability of encountering a rich assortment of alien plants (Reichard & White 2001; Smith et al. 2006).

We captured fruit bats as they exited the roost cave in the Judean lowlands of central Israel (31° 40′ 58″ N 34° 54′ 34″ E), and equipped them with a tracking device combining a radiotelemetry unit (BD-2, Holohil Systems, Canada) and a lightweight GPS datalogger (GiPSy2, TechnoSmArt, Italy), together weighing 9.66 ± 2.3 g (mean ± SD; range 6.9–12.8 g) including batteries, protective casing and glue used to attach the device to the bat's back, approximately 4% to 9% of the tracked bat's total body mass (147.5 ± 11.1 g). From preliminary experiments, GPS accuracy was estimated to be lower than 5 metres 95% of the time, enabling us to track the exact route of the bat to a specific tree. All bat captures and tracking were approved by the Hebrew University of Jerusalem ethics committee and the Israel Nature and National Parks Protection Authority (licence 33060 given to A.T.). Ten bats were tracked throughout the entire nightly foraging excursion in a high spatiotemporal resolution of 0.1–1 Hz ($n = 9$) or once every 3 minutes ($n = 1$). The tracking device fell off the bats within 1–5 weeks from the time of attachment and was collected for data retrieval.

Tracked fruit bats exhibited long ($14,491 \pm 4,160$ m), straight (straightness index: 0.95 ± 0.04) and fast (33.4 ± 3.1 km/h) continuous commuting flight in relatively high altitudes above ground level (130.7 ± 50.3 m) upon departing from their roost after sunset and while flying back from the foraging site to the roost before sunrise, and showed a consistent foraging pattern where they feed mainly during the start and end of the night.

The bats' foraging site was found to constitute a relatively small area with a median convex hull of 0.052 km^2 per bat. The fruit bats showed a strong preference for foraging near human settlements (Monte-Carlo, $P < 0.001$. The test was conducted by averaging the distances of a set of random points from their nearest settlement centre within the potential foraging area of the bats (a circle of 21 km radius around the roost), repeating this 10^6 times and comparing the distribu-

tion created by the simulations with the measured mean distance from the bats' foraging sites to their nearest settlement centre (795 ± 490 m)). Each tree visited by the tracked bats was identified to the species level and was assessed for fruit fecundity and ripening (see text of Fig. 9.2 for a list of fruit tree species visited by the bats). A foraging event was defined only if the bat had landed for longer than 1 minute on a tree with ripe fruits. The fruit bats were generalist feeders, showing no preference for native or alien species (*t*-test; $t = 0.686$, $P = 0.515$). Gut retention time (GRT) was tested in a set of standard laboratory experiments (Sun et al. 1997; Holbrook & Smith 2000) on 13 individual wild bats from a recently established captive colony. They were offered two different fruits, selected to represent common plants endozoochorously dispersed by bats (Izhaki et al. 1995): the native common fig (*Ficus carica*) and the naturalized white mulberry (*Morus alba*), which is considered invasive in other parts of the world (Global Invasive Species Team, The Nature Conservancy: www.nature.org). We assumed both fruit species are consumed similarly by the bats, as indicated by field observations. GRT, representing all swallowed and defaecated seeds, was calculated and a gamma function was fitted for each of the two fruit species separately and for all data pooled together. Mean GRT was 55 minutes (range 16–414 minutes) for *F. carica* and 47 minutes (range 18–105 minutes) for *M. alba*. The fitted GRT gamma distributions were significantly different between the two species (Kolmogorov–Smirnov two-sample test; $Z = 3.902$, $P < 0.001$). Mean GRT for all data pooled together was 53 minutes.

Bat-generated dispersal distance kernels were calculated by multiplying the probability that the bat is located at a certain distance from the source tree at a certain time after feeding (based on the tracking data) and the defecation probability of a seed at that time (estimated from the fitted GRT gamma function). We separated the movement data of the tracked bats into two groups, according to the fruit trees they visited, and calculated four dispersal distance kernels from the different GRT distributions (Fig. 9.2): (i) alien, naturalized and invasive tree species with the pooled (*F. carica* and *M. alba*) GRT distribution; (ii) native tree species with the pooled GRT distribution; (iii) all trees with the GRT distribution for *F. carica* alone; and (iv) all trees with the GRT distribution for *M. alba* alone. Although the fitted GRT functions differed between the naturalized *M. alba* and the native *F. carica*, the dispersal dis-
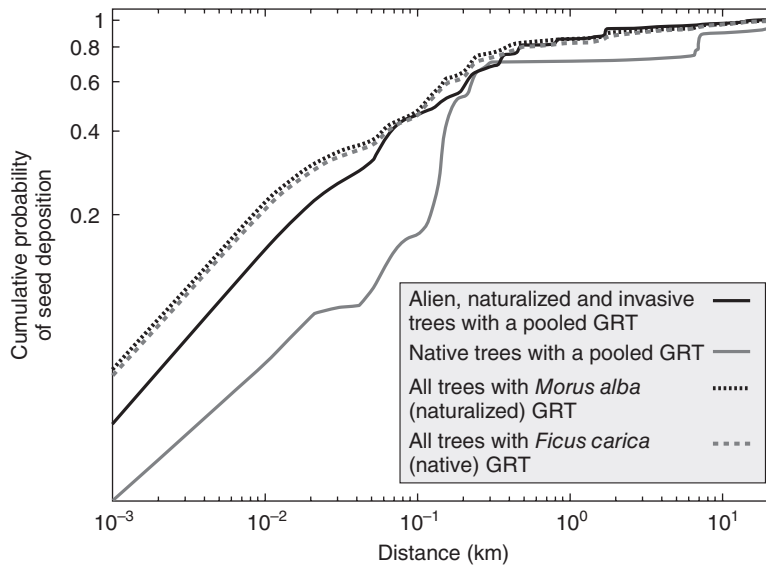
Fig. 9.2 Dispersal distance kernels of bat-dispersed seeds: the cumulative probability of seed deposition, calculated separately for the alien, naturalized and invasive tree species group (*Ficus sycomorus*, *Morus alba*, *Melia azedarach*, *Phoenix dactylifera* and *Washingtonia* sp., solid black line) and for the native tree species group (*Ficus carica*, *Ceratonia siliiqua* and *Olea europaea*, solid grey line) both using the pooled GRT distribution (see main text). The dotted black and grey lines represent the cumulative probability of seed deposition calculated for all trees using the GRT distribution of *M. alba* and *F. carica*, respectively.

tance kernels representing groups (iii) and (iv) were almost identical (Fig. 9.2, dotted grey and black lines), indicating that, controlling for the spatial movement of the vector, the difference in GRT had very little effect on the dispersal kernel. This result indicates that, in this case, seed dispersal distance is not as sensitive to the measured variation in GRT as was expected. In contrast, differences in the spatial distribution of the trees between group (i) and (ii) had a considerable effect on the kernels (Fig. 9.2, solid grey and black lines), which differed significantly (Kolmogorov–Smirnov two-sample test; $Z = 5.233$, $P < 0.001$). A spatially explicit simulation of bat-dispersed seeds revealed that what might be conceived as a simple seed shadow (the spatial distribution of seeds originated from a single source) around each tree is actually a complex mixture of overlapping seed shadows generated by the foraging bat. That is, the seed rain around a fruiting tree commonly encompasses seeds taken from other trees in the neighbourhood, and multiple-source 'seed shadows' are generated even in the vicinity of roosts and non-fruiting resting trees (Fig. 9.3). Although bats are predicted to disperse many (43.9%) seeds near (0–100 metres) the source plant, a high portion (17.2%) of seeds are dispersed long (more than 1 km) distances of up to 20 km (Fig. 9.2), owing to their fast and long commuting flights.

In summary, the Egyptian fruit bats act as both local and LDD vectors of both native and alien seed species. The local dispersal generates seed aggregations around source trees, whereas LDD tends to generate remote seed aggregations elsewhere. The surprising prediction that bats generate aggregations of long-distance dispersed seeds, rather than isolated individual events, can be attributed to the substantial proportion of LDD events. This is facilitated by several characteristics of the fruit bat, such as its fast and straight commuting flights to foraging sites far away from the main roost and its tendency to rest for a long time on non-fruiting trees and outside its main roost, providing new establishment opportunities for dispersed seeds away from the source plant. The landscape structure, or more specifically the spatial distribution of the fruit trees, rather than gut retention time, had the strongest effect on the dispersal kernel. Fruit bats exhibited a generalist habit to eat fruits from a wide range of plant species, readily feeding on alien plants. Their role as dispersers of potentially invasive species is further emphasized by their tendency to forage near human settlements where the initial introduction of invasive species is most expected. Altogether, our findings illustrate that understanding the movement ecology of the dispersal vector is mandatory for understanding and predicting the spatial dynamics of invasive, or potentially
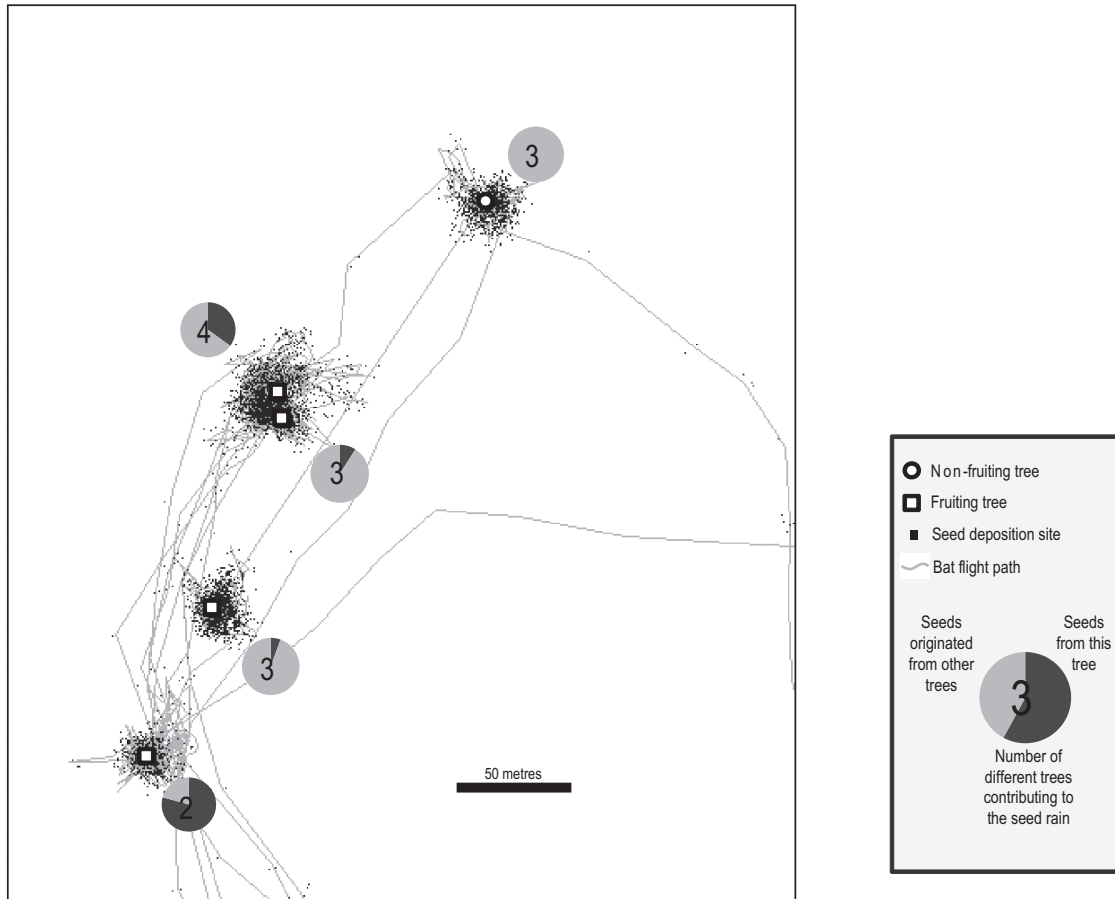
Fig. 9.3 An example of overlapping seed shadows (black dots) predicted for a full nightly path of a foraging bat (grey lines). The pie charts portray the proportions of seeds deposited in a radius of 10 m around a tree that have originated from this tree (dark grey) or from other trees (light grey). The number within the pie chart represents the total number of trees that contributed to the seed rain around each tree. White squares and circles represent fruit and non-fruit trees, respectively. Notice the upper tree is not a fruit tree but has a seed shadow similar to that of the fruit trees.

invasive, plant species (see also Murphy et al. 2008; Westcott et al. 2008). We note, however, that these findings might be specific to our study system and generalizations about the role of fruit bats in driving invasive spread should await data from different plant species and other systems as well. We emphasize again that invasion success strongly depends on post-dispersal processes that determine the survival and establishment of dispersed seeds, an important phase in a plant life cycle (Nathan & Muller-Landau 2000; Wang & Smith 2002), not elaborated in this chapter.

9.5   CONCLUSIONS

Five decades since the publication of Elton's book have witnessed new tools and concepts developed to study seed dispersal. Elton has identified humans' overriding role as the most pronounced dispersal vector responsible for the entry stage of current invasions; yet dispersal is also critically important in the establishment and spread stages of successful invasions, being a major factor in determining the spatial dynamics of plant populations. The dispersal ability of plant species

strongly relies on the movement properties of the dispersal vector. Thus, to advance our understanding of the factors and mechanisms influencing seed dispersal and invasion processes, a vector-based approach should be promoted. Here we illustrate the application of a twofold nested design of the movement ecology framework to study dispersal of native and alien fleshy-fruited plant species dispersed by a generalist frugivore, the Egyptian fruit bat. We found that bats fly long distances to restricted foraging sites, generate complex seed shadows with peaks at the vicinity of both fruiting and non-fruiting trees, and are likely to play a key role in dispersing potentially invasive species as LDD vectors exhibiting strong preference to forage near human settlements. We have also shown in this case that the dispersal distance kernel is more strongly affected by the spatial distribution of the fruiting trees, than by the differences in gut retention times among the native or alien plant species examined. The mean and maximum distances of seed dispersal by the fruit bats are much higher than the corresponding dispersal distances expected from allometric relationships, even though their flight speed and gut retention time are relatively similar; the Egyptian fruit bat (presumably like many other fruit bats) is thus exceptional among mammals in its mean seed dispersal distance, even compared with flying frugivorous birds.

Our take-home message emphasizes the need to elucidate the movement ecology of any potentially invasive organism for understanding invasion processes and reducing associated hazards. Understanding the interactions between the plant and its vector should improve our ability to manage and prevent the establishment and spread of invasive species. In our case study, the habit of fruit bats to aggregate in large roosts opens opportunities for monitoring invasion processes by identifying new alien species of seeds in the bat guano dropped within the roosts, while reducing fruit bat activity within settlements could reduce their ability to disperse seeds of plants that have just passed the preliminary entry stage.

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