Foraging movements and navigation capacity of Egyptian fruit bats (*Rousettus aegyptiacus*), and their role in seed dispersal

A thesis submitted for the degree of

“Doctor of Philosophy”

by

Asaf Tsoar

Submitted to the Senate of the Hebrew University

December 2011

This work was carried out under the supervision of Prof. Ran Nathan.

Acknowledgements

I want to express my deepest gratitude to the following colleagues, mentors, supervisors and institutions for their invaluable help that made this work possible:

Ran Nathan, my devoted supervisor, who was an inspiration to me and has taught me how to think and work as a scientist. I am also very grateful to him for enabling me the freedom to "wonder around" and test new possibilities while keeping me on track.

Nachum Ulanovsky, for his crucial help, friendship and most beneficial discussions.

My thesis advisory committee: Ido Izhaki, Uzi Motro and David Saltz for their advice and encouragements.

Yoav Bartan and Ofir Altshtein, for their technical help in the field and in the lab.

Adi Ben-nun, for his assistance with spatial analysis and GIS, and for his wonderful friendship during these years.

Ronen Kadmon, my former M.Sc. advisor, for his appreciable advice and support and for teaching me critical thinking.

Sarit Levy and Ada Goldman-Asulin, for their administrative help.

Giaccomo Delomo and Alexi Vissotzki, for their advice and technical support.

Yossi Yovel, Luba and Tal Avgar, Orr Spiegel, Shalev bodenhimer, Netta Shalev, David Shohami, Nir and Nirit (and Pugi) Sapir, Ofer Steinitz, and Amram Zabari for their practical field assistance.

Yossi Yovel, Nir Sapir, Orr Spiegel, Ofer Steinitz, Tal and Luba Avgar, Carmi Korine, Amit Dolev, David Makin, Eran Levin, Yoram Yom-Tov, Benny Shalmon, Marc Holderied, Paul Racey, Gareth Jones, Brock Fenton and Tom Kunz, for fertile discussions.

Illan Shifman, ranger, Israel Nature and Parks Authority,and Sharon Tal, Bet-Guvrin National Park, Israel Nature and Parks Authority, for their support.

Gila Kahila Bar-Gal, for teaching me the secrets of molecular work.

Yotam Orchan, for his assistance in finding and retrieving GPS devices and hidden

roosts.

Nir Horvitz, for his useful assistance in spatial analysis of GPS data and MatLab.

Israeli Fruit council, Ministry of Agriculture, for GIS data on fruit plantations

Yaakov Lorch for fascinating talks and editorial help.

Ron Elazari-Volcani, for assisting with bat marking experiments.

Yoel Melamed, Hagar Leshner, Avinoam Danin, Miriam Ron, and Avi Shmida, for their help with plant and seed identification and interesting talks.

Boris Shirman,Survey of Israel, for magnetic data.

A special thanks to Nissim Amsalem, of the Israeli Air force, for his helpful aid in finding and monitoring one of the biggest fruit bat colonies in the area.

Yehudah L. Werner, for valuable talks on our way to and from the university.

Nechama M. Ben-Eliahu, for editing the manuscript.

Yakov Lorch for editing previous versions of the thesis.

Yehoshua Shkedy and Raviv Shapira, the Israel Nature and Parks Authority, for giving me the time to wrap up this work.

Special thanks to my parents, Sarah and Haim Tsoar and to my sister Hila Tamir, for their endless support and assistance.

I am in gratitude to the following organizations for their financial support: Bat Conservation International, the Lubee Bat Conservancy, the Zoological Society of Israel, and the Rieger–Jewish National Fund Foundation.

This study was funded by Israel Science Foundation (ISF) Grants ISF-FIRST 1316/05 and ISF 1259/09;

Last but not least…

To my beloved wife Dana, your support, advice and huge endeavors have undoubtedly made this work possible, and to my beautiful and amazing daughters (who have all been born during the thesis), Tamar, Hadas and Rotem, for making your father so proud and happy…

Abstract

Movement is one of the fundamental features of life on earth. Many animals move regularly to effectively find and consume food and to actively improve the quality and quantity of their food intake. A foraging animal must acquire information about its environment to decide where and when to forage, as well as how to move from one place to another. Plant-frugivore relationships play a key role in the dynamics of ecological systems and in the evolution of animal and plant traits. These interactions determine the movement of frugivores and the dispersal of plant seeds.

This thesis comprises three distinct, yet related chapters that deal with the movement ecology of the Egyptian fruit bat (*Rousettus aegyptiacus*). Chapter 1 describes the study of the daily foraging movements of individuals in relation to the distribution of their food resources (fruit trees) using spatial analyses of landscape features and GPS tracks of the bats. Chapter 2 describes the investigation of the navigation capacity of bats, based on different sets of homing experiments on GPS-tracked individuals. Finally, in Chapter 3, the potential role of the bats as long-distance dispersers of plant seeds is elucidated, from computer simulations of an empirically-calibrated mechanistic seed dispersal model, and the bats potential as a vector of invasive species is evaluated.

The movement of bats is the unifying concept of this thesis. I studied the patterns (Chapter 1), the underlying mechanisms (Chapter 2) and the consequences of the movements of individual bats (Chapter 3). The conceptual framework of movement ecology puts these three chapters in a unifying template. This framework asserts that four basic components are needed to describe any type of movement by any organism: (1) the internal state from which the individual’s motivation to move is derived; two constraints – (2) the navigation capacity, and (3) the motion capacity – of the individual organism that reflect, respectively, the mechanisms used to execute movement and to decide where and when to move; and (4) the broad set of biotic and abiotic external factors affecting each of the components above. The interplay between these four

components shapes the movement path, which in turn affects the internal state of the bats and the external factors governing their movement. Here I explore a variety of links in the movement ecology framework. In chapter 1, I focus on the relationships between the daily need to consume food (internal state) and the distribution of food resources (key external factor). In chapter 2, I focus on how bats return home (internal state) after translocation to remote sites (navigation capacity). In chapter 3, I employ a nested design of the movement ecology framework, in which the movement ecology of the plants is nested within the movement ecology of the bats. Here, the bats are the key external factor for the movement of the seeds, and the trees and fruits are the main external factors determining the movement of the bats.

I combined various research methodologies to quantify the movement of the bats, to explore their navigation capacity and to estimate the consequences for plant dispersal. These include bio-telemetry techniques, homing field experiments, laboratory experiments, computer simulations and spatial analyses. The principal methodology applied in all parts of my work is global positioning system (GPS) telemetry. Recent miniaturization and power reduction in GPS technology enabled the acquisition of accurate data on the movements of bats over relatively large scales and with high spatiotemporal resolution. Using a miniature GPS data logger, I collected 3D location data of 74 individual bats. Sixty nine bats were recorded at a fix rate of 1Hz and five at a fix rate of once every 1–3 minutes. Bats were tracked for > 9 hours and up to several successive nights. An additional 26 bats were tracked using radio telemetry by two to four tracking teams simultaneously. Bat location was recorded once every 2 minutes for up to a full night and from one to thirteen nights. Bat location was determined by triangulation of data from all the tracking teams.

In the first chapter of this thesis, I quantified the bat's foraging movement in regards to the landscape structure and the way bats optimize their foraging behavior. I first measured the bat's loyalty to its roost and found bats to show medium-high roost loyalty. I then described their foraging behavior and found that bats fly long distances (up to 25 km away from their roost) by a fast (median speed of 9.28 m/s), high (median height above ground 103.8 meters) and straight flight track (mean straightness index of

0.92). Bats showed loyalty to the visited fruit trees and commuting flight tracks. I have observed a general foraging pattern by the bats, where they forage by a long distance commuting flight to specific fruit trees, stay within their vicinity throughout the night and then return back to the roost before sunrise by a similar commuting flight track.

The landscape structure affected the spatial foraging pattern at the individual, as well as the population, level. The spatial distribution of the bat foraging population was similar to the distribution of resources within the landscape, yet the bats selected fruit trees that were significantly closer to the roost than would be expected purely by chance. The next stage in the research was to create a spatially explicit attractiveness model. The model's grain size was 1 km^2 and its extent was a radius of 25 km around the roost. Each cell was scored by its tree density divided by its distance from the roost. Through this simplified model, I found that bats foraged at high-scored cells, at a significantly higher rate than by random selection or if the bats would have selected the fruit trees of the same species and ripeness as the trees they eventually did select, but that were the closest to their roost. By energetic modeling I also found that bats minimized energetic flight expenditure by applying a commuting flight speed requiring minimum power.

The long distance foraging flights quantified in Chapter 1, suggest that the bats possess a keen spatial memory of their foraging area, and are capable of navigating easily to distant locations. To examine the navigational capacity of the bats and to shed light on the possible underlying mechanisms, I carried out several homing experiments. In the first experimental set, the bats were translocated 44 km south of their roost, well beyond their typical foraging area. By manipulating feeding and release time, I found the bats oriented to one of two destinations: hungry bats released early during the night oriented directly to a feeding tree, while well-fed bats released late at night, oriented directly to their roost. In the second set of homing experiments, I released the bats 84 km south of their roost, within and above a deep natural erosional crater. The bats were initially disoriented, but eventually left the crater toward the home direction and homed successfully. Bats released at the crater edge homed directly. These results suggest navigation guided by distal visual landmarks, providing evidence for large-scale navigation of a mammal within its visually familiar area. Yet, the fact that all disoriented bats left the crater in a northerly direction demonstrate their ability to home without visual cues, thus indicating an additional navigation mechanism, possibly using geomagnetic and/or olfactory cues as indicated by recent findings of a possible magnetic sense in insectivorous bats.

As the two previous chapters have shown, bats may carry out long distance foraging flight commutes and thus have potential as long-distance dispersal (LDD) vectors of plant seeds. The third chapter of my thesis investigates the role of the fruit bats as seed dispersal vectors and examines how motion and navigation capacities affect their potential to disperse seeds of plants in general and invasive plants in particular. Based on the foraging movements and gut retention time quantified in this thesis, I developed a simulation model to assess seed dispersal by the bats in a spatially explicit context. I found that bats generated complex seed shadows and fat-tailed dispersal kernels, dispersing seeds to distances of up to 20 km with peaks in the vicinity of both fruiting and non-fruiting trees. I also found that bats strongly prefer to forage near human settlements. I thus conclude that Egyptian fruit bats are likely to play a key role in dispersing potentially invasive species as LDD vectors. I also showed that the dispersal distance kernel is strongly affected by the spatial distribution of the fruiting trees, rather than by the differences in gut retention times of seeds of the native or alien plant species examined.

In the third chapter I also quantified, for the first time, the allometric relationships between the mean and the maximum seed dispersal distances and the body mass of both flying and non-flying frugivorous vertebrates (birds and mammals) that disperse fleshy-fruited plants by endozoochory. Both the mean and the maximum distances of seed dispersal by the Egyptian fruit bats, as estimated in my thesis, are much higher than the corresponding dispersal distances expected from the allometric relationships, even though their mean flight speeds and gut retention time are similar to those of birds. The Egyptian fruit bat is thus exceptional among mammals in its mean seed dispersal distance, even when compared with flying frugivorous birds.

This study has multiple implications for landscape management and conservation.

For example, the finding that bats forage long distances and are loyal to specific fruiting trees implies that damage to commercial orchards can be addressed efficiently by capturing the specific bats visiting that orchard. The findings regarding the bats' potential as a vector of invasive species should be further investigated for practical implications of ecosystem management.

There are several traits that make the Egyptian fruit bat a great model animal for movement and navigation research: it is common, relatively large, easy to rear and train, it is highly social, flies to long distances and has a strong motivation to return to its original colony, similar to carrier pigeons.

This thesis has investigated different aspects of movement ecology in the Egyptian fruit bat, using innovative technology never before used on bats. This is undoubtedly the start of a fascinating era in movement ecology research of medium and small animals in general and bats in particular. Future research should address, among other things, the question of what are the additional cues used by the bats for their long distance navigation and also how the social interaction between individuals affects their foraging and navigational ability.

TABLE OF CONTENTS

1. GENERAL INTRODUCTION

Movement of organisms is one of the most basic features of life. It is an important component of almost any ecological and evolutionary process and plays a key role in determining the fate of individuals, the structure and dynamics of populations, communities and ecosystems, as well as the evolution and diversity of life itself, habitat fragmentation, changes in land-use pattern and climate, and the introduction of exotic species (Nathan *et al.* 2008a). Therefore, movement research is of crucial importance for both basic and applied science (Baker 1978; Swingland & Greenwood 1983; Stenseth & Lidicker 1992; Dingle 1996; Clobert *et al.* 2001; Isard & Gage 2001; Bullock, Kenward, & Hails 2002; Levey, Silva, & Galett 2002; Greenberg & Marra 2005). Movement research is characterized today by a broad range of specialized scientific approaches, each developed to explore a different type of movement carried out by a specific group of organisms. The emerging ˝movement ecology˝ discipline (Nathan *et al.* 2008a) catalyzes the integration of movement research by elucidating the principal components of movement.

The present thesis describes studies of the movement ecology of the Egyptian fruit bat, divided into three distinct yet related chapters. Chapter one focuses on the relationships between the bat’s daily need to consume food (internal state) and the distribution of food resources (key external factor) within the landscape, while being restricted by its roost location (external factors) and the energetic cost of foraging flights (internal state). Chapter two focuses on how bats return home (internal state) after translocation to remote sites (navigation capacity)(Schurr *et al.* 2010; Tsoar *et al.* 2011a). In Chapter 3, I examine how the movement of the bats affects the movement of other organisms. To this end, I developed a nested design of the movement ecology framework, in which the movement ecology of the plants is nested within the movement ecology of the bats, and the bats are the key external factor for the movement of the seeds, while the trees and fruits are the main external factors determining the movement of the bats (Tsoar *et al.* 2011a).

The common theme of all three chapters in this thesis is the movement ecology of the Egyptian fruit bat, describing its movement pattern and navigation ability, the factors affecting it and how all these factors are expected to impact other organisms.

Animal movement and movement ecology

Animal movement, defined as the change in the spatial location of the whole individual in time, is driven by processes that act across multiple spatial and temporal scales, which are being studied in multiple research disciplines (Swingland & Greenwood 1983; Schick *et al.* 2008). Animals may move during their entire life or during specific seasons or life stages. They are known to move various distances, from several centimeters during their entire life to crossing the globe twice a year. Movement research has been estimated to produce 26,000 papers in the 1997-2006 decade, increasingly growing in both in number and proportion over this period (Holyoak *et al.* 2008). This progress parallels a recent boost of technological advancements such as satellite-tracking using the Argos system, geo-tagging or tracking units based on Global Positioning Systems (GPS), that have recently revolutionized the quality, quantity and scale of animal tracking data in the wild (see Bridge et al., (2011) for a recent review. The development of movement ecology is strongly enhanced by the advances in animal tracking and bio-logging techniques, making it possible to track multiple individuals in greater accuracy and for longer times compared with what was feasible only a few years ago. This, in turn, has also improved the input parameters inserted into models of animal movement (Jonsen, Myers, & Flemming 2003; Jonsen, Flenming, & Myers 2005; Hebblewhite & Haydon 2010). Currently, the main restriction in animal tracking is the need for energy, as well as the maximum mass of a tracking device attached to an animal. Recent advancements have reduced tag energy consumption as well as the mass of the tracking devices (Bowlin *et al.* 2010; Robinson *et al.* 2010). As illustrated in this thesis, such technological advancements enable us to address important questions about animal movement that were out of reach just a few years ago. In particular, in the present study, I have implemented cutting-edge GPS technology capable of recording movement at a very high spatial and temporal resolution (Steiner *et al.* 2000; Biro *et al.* 2002) to track, for the first time, a wild flying mammal, the Egyptian fruit bat (Tsoar *et al.* 2011a; b).

The recent Movement Ecology framework defines the basic mechanisms of movement by all organisms within a single unified framework (Nathan *et al.* 2008a). It asserts that four basic components are needed to describe any type of movement by any organism. The first is the internal state ("why move?") of the individual that affects its motivation to move. It accounts for the physiological and psychological state of the individual driving it to move. The second is the navigation capacity ("when and where to move?") of the organism that accounts for its ability to orient in time and space. The organism might be restricted in its movement due to cognitive or sensory limitations of this component. The motion capacity ("how to move?") is the ability of the organism to move in space and time; it includes the mechanisms used to execute movement. The external factors ("which factors effect movement beyond those directly related to the individual?") comprise a broad set of biotic and abiotic factors, external to the organism, affecting each of the three components above. The aim of the movement ecology conceptual framework is to articulate and then integrate these four components that produce the movement of an individual organism.

When accounting for individuals moving with the aid of other organisms, we need to consider a nested design of the movement ecology framework, in which the movement ecology of the assisted organism is nested within the movement ecology of the organism that transports it. Such a nested design will be further elaborated in chapter 3 of this thesis.

The generality of the movement ecology framework facilitates the comparison between different organisms (Holyoak *et al.* 2008) and among movement phenomena: in chapter 1, I apply it to studying the foraging of bats, and in chapter 3 to studying the dispersal of plants. The framework can also be used to highlight particular components such as navigation capacity, investigated in chapter 2. It can also guide the development of mechanistic models exploring how movement of individuals modulates the interactions among trophic levels; this is illustrated in chapter 3, focusing on the role of bats in dispersing plant seeds.

Animal foraging: central-place foraging

Many animals are highly mobile, moving on a daily basis from very local to global scales in search of food and other resources. Foraging is one of the most basic and common movement phenomena; it is defined by the Oxford dictionary as to “search widely for food or provisions”. Foraging research encompasses observations, experiments, and modeling (Stephens & Krebs 1986), and its theoretical basis is found in the theories of economics and human behavior. A fundamental tenet in optimal foraging theory postulates that animals maximize their gain relative to cost while optimizing their energy balance during foraging (Stephens & Krebs 1986). In general, optimal foraging theory predicts that animals should select the most energetically rich fruit trees (gain) in relation to travel distance (cost) while maximizing their net energy gain (benefit). This simple principle is typically violated by considering predation risk, competition among conspecifics, alternative drivers of foraging movements (e.g., social interactions, learning, territorial defense) and alternative gains from food resources (e.g., certain nutrients or minerals) (Pyke 1984; Pierce & Ollason 1987). Notwithstanding the importance of such complications, the basic principle of optimal foraging provides a general context for studying animal foraging behavior. Such studies are often conducted under controlled conditions(Rosenzweig & Abramsky 1997; Katz *et al.* 2010) to rule out potential deviations from this basic principle, or to explicitly investigate one (or more) of these complications. Yet, the challenge of assessing whether this basic principle of optimal foraging can explain a large part of the variance in animal behavior in non-manipulated free-ranging animals is yet to be met.

Central-place foraging (CPF) occurs when the foraging movement of the animal is constrained by its need to return to a specific location or refuge (i.e., a nest, perch or roost) (Orians & Pearson 1979; Olsson, Brown, & Helf 2008). This constraint changes the optimal energetic considerations of the foraging animal, mainly by limiting its search duration and area (Bovet & Benhamou 1991; Olsson *et al.* 2008). It poses a major restraint on the foraging animal, restricting its movement and thus altering the costs and gains of its foraging movement (Rosenberg & McKelvey 1999; Matthiopoulos 2003). Thus, examining the foraging strategy of a central place forager requires considering how such restraints affect movement. A CPF animal might not exploit the most profitable resource patch due to high travel cost from the refuge to that resource (Rosenberg & McKelvey 1999; Matthiopoulos 2003). For our understanding of the CPF, we should understand the movement restraints, landscape structure, as well as the distribution of the resources within the landscape. Such information is hard to obtain and in most cases a simulating model is used instead (Matthiopoulos 2003).

The Ideal free distribution (IFD) theory predicts optimal foraging animals to be distributed in a spatial pattern that will enable each of individuals to acquire the same food intake, thus, on the population scale, it is predicted that distribution of individual foragers will reflect the distribution of the key resources. The theory assumes that foraging animals have full knowledge (thus, “ideal”) of the resources surrounding it and have no limitations or costs (thus, “free”) when moving between food patches (Fretwell & Lucas 1969; Fretwell 1972). Empirical work has shown that often these assumptions are violated and additional considerations cause the individual forager to behave differently than as predicted by theory (Kennedy & Gray 1993; Tregenza 1995; Krivan, Cressman, & Schneider 2008).

Most fruit bats are known to be generalists and to show plasticity in their food preference (Mcdonald-Madden *et al.* 2005), they are known to fly long distances in extremely patchy habitats (Cosson, Pons, & Masson 1999; Henry, Pons, & Cosson 2007); in some cases, bats were even found to forage between islands in the Pacific Ocean (McConkey & Drake 2007). While in recent years several studies have been carried out to quantify their flight (Riskin *et al.* 2010), none of these studies have examined optimal foraging of bats in natural conditions. To be able to forage between such remote locations, the bats must have a profound navigational system. To date, no research has been done on the navigational movement of bats (Holland 2007).

Animal navigation

Foraging animals need to find their food resources, and CPFs need to navigate between the foraging site and the central place/site. Navigation is defined as the ability to move non-randomly in space to reach desired goal locations using environmental cues or based on spatial memory (Wallraff 2005). The ability to navigate is critical to a plethora of animal activities including searching for food and mates, escaping predators and avoiding other risks, defending territories, and migrating long distances. It has been extensively studied in animals, mostly in non-mammalian species including bees, ants, fish, birds, and some marine vertebrates and invertebrates (Srinivasan *et al.* 2000; Cochran, Mouritsen, & Wikelski 2004; Lohmann *et al.* 2004; Menzel *et al.* 2005; Wallraff 2005). These studies revealed that animals use a wide range of cognitive strategies and environmental cues for navigation. For example, pigeons were shown to use magnetic cues in addition to celestial and visual cues for both short- and long-range navigation (Wallraff 2005). However, we are still far from assessing the navigational performance and elucidating the underlying mechanisms in other taxonomic groups, especially in mammals.

Griffin (1964) has defined three types of navigation abilities. The most advanced type includes a “navigational map”, that is, the ability to travel directly to a certain destination from any starting point within the environment, regardless of its direction and without relying on familiar cues or routes. The map and compass theory asserts that such a superb navigation ability requires a two-stage process during which the animal first places its current location in a “global” spatial context, and then uses environmental cues to return to its destination (Wiltschko & Wiltschko 2003; Wallraff 2005) although see Bingman & Cheng (2005) for an updated perspective on global navigation. Evidence for the existence of such a navigational map (Perdeck 1953) comes from field and laboratory experiments. In the field, homing experiments in translocated lobsters (Boles & Lohmann 2003), and pigeons (Baldaccini, Benvenuti, & Fiaschi 1976; Wallraff 2004), showed an ability to navigate from an unfamiliar site to one or more goal locations. Typically, inferences from such homing experiments were based either on animals’ vanishing bearing at the release site, or animals’ reappearance at the goal location. Only recently were translocated pigeons and honey bees tracked continuously (Lipp *et al.* 2004; Menzel *et al.* 2005). Yet, to date, no high-resolution movement tracks have been collected from free-ranging mammals homing from translocation distances greater than a few kilometers, and the lack of such data severely limits our understanding of mammalian navigation mechanisms. In the laboratory, studies implementing various experimental approaches suggested the existence of a mental representation of space, or a “cognitive map,” in rodents (Tolman 1948; Morris *et al.* 1982; Gallistel 1990). However, our ability to infer map-like navigation from laboratory experiments on such a small spatial scale (in meters) has been questioned (Bennett 1996; Ulanovsky & Moss 2008). Thus, there is a gap in our knowledge about mammalian navigation: most of our knowledge of large-scale navigation comes from studies of non-mammalian species, whereas detailed data on mammals’ navigation in the field is scarce, certainly as compared with data on birds. In chapter 2, I have shown bats to successfully orient themselves from locations far from their familiar area. Such long distance navigation implies that these bats can easily orient within their familiar area enabling their long distance foraging flights as described in chapter 1. The bats’ long distance foraging movement has important implications regarding their ability to forage within a fragmented habitat as well as their effect on the organisms they carry with them, such as seeds digested within their gut (Shilton *et al.* 1999; McConkey & Drake 2007).

The role of bats as seed dispersers

The two preceding sections, focusing on how bats forage and navigate, provide the background for studying the potential of the bat as long distance dispersal (LDD) vector of plant seeds in general, and invasive plant species in particular.

Seed dispersal is a key process in the dynamics and structure of populations, communities and ecosystems around the world (Nathan & Muller-landau 2000; Levin, Muller-landau, & Nathan 2003). Because plants are sessile, their dispersal is typically aided by an external vector (Howe & Smallwood 1982; van der Pijl 1982). Plant-frugivore relations cross trophic levels and are found to be extremely complicated (Marshall 1983; Shanahan *et al.* 2001; Levin *et al.* 2003; Bolmgren & Eriksson 2005). Its evolutionary importance is seen by the many dispersal traits plants have, and by the morphological traits many frugivores possess (Herrera 1985; Bascompte *et al.* 2003; Nathan *et al.* 2008a). The traditional focus of seed dispersal research on plant dispersal traits has recently shifted towards an emphasis on the crucial importance of vector traits (Jordano *et al.* 2007; Nathan *et al.* 2008a; Schurr, Steinitz, & Nathan 2008; Will & Tackenberg 2008). There are three mechanistic phases in passive dispersal of seeds by an animal: the vector seed load, displacement velocity and seed passage time (Nathan *et al.* 2008a; Schurr *et al.* 2010). Generalist frugivores are expected, by definition, to feed from a wider range of plant species (Nathan *et al.* 2008b); consequently, they have a higher potential than specialists to feed on and disperse invasive plant species (Buckley *et al.* 2006; Hulme *et al.* 2008).

Approximately 250 species of bats worldwide from the paleo-tropical family, Pteropodidae, and the neo-tropical family, Phyllostomidae, regularly visit plants for either fruit or floral resources and depend heavily on plant resources throughout the year (Heithaus et al., 1975; Marshall, 1983; Fleming, 1988; Cosson et al., 1999; Shanahan et al., 2001; Muscarella and Fleming, 2007). Fruit bats have been found to forage at distances ranging from a few hundred meters and up to 40 km per night, to migrate over long distances (Tidemann & Nelson 2004; Richter & Cumming 2005; McConkey & Drake 2007; Smith *et al.* 2011) and are known to be important pollinators and dispersers of seeds mainly within the tropical region (Fleming & Heithaus 1981; Marshall 1983; Fleming 1988; Fujita & Tuttle 1991; Mickleburgh, Huston, & Racey 1992; Kalko, Herre, & Handley 1996; Shilton *et al.* 1999; Tan, Zubaid, & Kunz 2000; Shanahan & Compton 2001; Hodgkison, Balding, & Kunz 2003; Ingle 2003; Henry *et al.* 2007; Muscarella & Fleming 2007; Kunz *et al.* 2011). Yet, little is known about the seed dispersal potential of bats outside the tropics. Foraging of the Egyptian fruit bat, the only fruit bat of the Palearctic region (section 1.5), has been studied in Israel (Makin 1990; Izhaki, Korine, & Arad 1995; Korine, Izhaki, & Arad 1998, 1999). Yet, the basic descriptors of the seed dispersal process, the seed dispersal kernel generated by the bats, and the potential of the bats to disperse viable seeds across the landscape, have not yet been quantified. In chapter 3, I used movement data collected from free-ranging foraging bats, and conducted laboratory experiments on gut passage time (Sun *et al.* 1997; Loiselle & Blake 1999; Holbrook & Smith 2000), to assess the seed dispersal kernel and the spatial seed deposition patterns generated by the Egyptian fruit bat.

The study of allometric relationships between body size (or mass) and factors such as metabolic rate and cost of movement has advanced many fields of ecology and evolutionary biology (Calder 1984; Schmidt-Nielsen 1984; Robbins 1993). Yet, allometric principles have not been applied to predict the basic metrics of seed dispersal by animals. Such allometric relationships can be assessed from known relationships between body mass and relevant animal traits and characteristics affecting seed dispersal (Calder 1984; Schmidt-Nielsen 1984; Robbins 1993). Animals with larger body mass are predicted to have larger home range, higher travel velocities and longer seed retention times, compared with smaller animals within the same taxonomic group (Calder 1984; Schmidt-Nielsen 1984; Robbins 1993). Larger animals are therefore expected, by allometric relations alone, to disperse seeds to greater distances. Moreover, large animals often take up seeds of a wide variety of plant species, irrespective of their dispersal morphology (e.g. Westcott et al., 2005). My contribution to the publication of Schurr et al. (2010) was a meta-analysis of endozoochorous dispersal by birds, showing that seed dispersal distance increases with the body mass of avian dispersers as predicted by allometric relationships. Furthermore, I developed a simple general model that relates the body mass of animals to the mean dispersal distance of the seeds they disperse by endozoochory. Such a model can be used to approximate mean dispersal distances from body mass alone, or serve as a generic model for the expected dispersal distances of species differing in their body mass. The model, further extended with additional data in chapter 3, will enable us to examine the potential contribution of the fruit bats to the general seed dispersal community of vertebrates.

The Egyptian fruit bat (*Rousettus aegyptiacus*) as a case study

The Egyptian fruit bat is one of the most common fruit bats within the Pteropodidae family. It is a medium sized bat (100–200 gram) with a wide distribution range from

South Africa to southern Turkey (excluding the Sahara) and as far as India in the east (Kwiecinski & Griffiths 1999). It is the only fruit bat species in the Palearctic region, and is a very common species in Israel, mainly in the Mediterranean region (Mendelssohn & Yom-Tov 1999). It has been suggested that, although common within its distribution range, the bats' population is mainly limited by the availability of suitable refuges. Lewis (1995) has shown that roost fidelity is inversely related to roost availability, and that bats roosting on tree branches, such as most species of the Pteropodidae family, are expected to switch roosts more often than cave-dwelling fruit bats of the Phyllostomidae family. The Egyptian fruit bat, unlike most members of its family, constrains itself to caves or artificial structures for day roosting (Kwiecinski & Griffiths 1999). The level of roost fidelity has never been quantified, but it is speculated to be a central place forager (Korine, Izhaki, & Makin 1994).

The Egyptian fruit bat is considered a generalist forager, feeding on almost all fleshy fruit trees within its range, including both invasive and natural plant species (Makin 1990; Izhaki *et al.* 1995; Korine *et al.* 1998, 1999; Kwiecinski & Griffiths 1999). As in most of its family members, its main senses are vision and smell (Raghuram *et al.* 2009), although unlike most of its family members, it does emit echolocation calls, but these calls are for very short range detection (Yovel *et al.* 2010). As with most bats, its natural enemies are mainly owls, raptors, and snakes (Fenton *et al.* 1994b). Although it is one of the most common fruit bats world-wide, little is known about its nightly foraging movements or its potential as a long-distance seed disperser. Jacobsen et al. (1986) documented foraging flights of up to 24 km, while Makin (1990) and Barclay & Jacobs (2011) found the bats repeatedly visit specific fruit trees. The Egyptian fruit bat is considered a non-migrant species across its range and in Israel in particular. Until the late 1980s, it was eradicated on the pretence of it being an agricultural pest causing damage to commercial orchards. Bats were killed in their thousands, and entire colonies were wiped out (Makin & Mendelssohn 1985, 1987). The bat culling was conducted in caves by pesticide fumigation. This act was the main cause leading to the reduction of insectivorous bats in Israel (Makin 1977, 1988). Since the 1990s the fumigation has stopped and *Rousettus* populations are increasing in many parts of the country. Today, there are hardly any complaints from farmers, although by law this species is still considered a pest in Israel, and has no legal conservation status (Korine *et al.* 1999).

Research objectives and outline of the dissertation

Bat movement is the unifying theme of my thesis: its patterns, the underlying mechanism and the consequences for plants. Here I define the objectives and the research questions for each of the three Results chapters:

In the first chapter (section 3.1), my goal was to examine whether the foraging movements of the bats fit the basic predictions of optimal foraging of central place foragers at the individual level and of IFD theory at the population level (see section 1.2). More specifically, my objectives were:

(1) To measure the nightly foraging movements of individuals in high spatial and temporal resolution and to assess the level of fidelity of the bats to their roosts and to specific food resources.

(2) To map the distribution of the food resources (fruit trees) at the individual tree level across the entire relevant area.

(3) To test whether the spatial distribution of foraging bats matches the spatial distribution of the resources within the landscape as predicted by the IFD theory.

(4) Assuming that (3) will provide evidence for CPF, to use the data obtained in (2) to assess the spatially explicit variation in resource attractiveness in terms of gain (food) versus costs (distance from the roost).

(5) To compare several features of bat foraging movements including foraging flights, stops and fruit trees they visited (available from (1)), against the corresponding expectations derived from the attractiveness maps (from (4)).

I predicted the Egyptian fruit bat would act as a central place forager, showing high roost fidelity, as expected for cave-roosting bats (Lewis 1995). Because fruit is spatially and temporally predictable within the Eastern Mediterranean landscape, I predicted that similar to other places in the world, the bats would show high fidelity also to specific foraging areas, as long as the trees have sufficient fruit on them (Fleming 1988). I thus predicted the bats would fly by a direct and repeated flight path to specific fruit trees and repeated on consecutive foraging events, as been found to happen in other bats (Morrison 1978a; Fleming 1988; Andrianaivoarivelo *et al.* 2011). I expected the bats to forage at sites where the resource attractiveness is the higher that average, based on optimal foraging theory. At the population level, I predicted that foraging bats would be distributed in a pattern similar to the density of fruit trees in the landscape, based on the IDF theory.

In the second chapter (section 3.2), I proceeded to investigate the navigation capacity of bats, based on different sets of homing experiments on GPS-tracked individuals. My goal here was to assess the navigational performance of fruit bats, and a possible environmental cue they use for orientation. More specifically, I set two objectives to carry out homing experiments of free-ranging wild bats designed:

1) To distinguish between the following navigational strategies: beaconing, route-following, directional orientation or map-like memory.
2) To assess the use of distal visual cues for long-distance navigation.

My predictions were that due to their long foraging flights, fruit bats possess a map-like memory. Owing to the bats’ high altitude commuting flight, I predicted that the bats use visual cues for orientation.

In the third chapter (section 3.3), my goal was to examine the potential role of the bats as LDD vectors of plant seeds, particularly of potentially invasive species. I set the following research objectives for this chapter:

1) To quantify gut passage time of seeds of native and invasive plant species consumed by bats.
2) To merge data from objective (1) of chapter 3.1 and objective (2) of this

chapter to develop a spatially explicit mechanistic model of bat-mediated seed dispersal of native and alien plant species.

3) To use the model developed in (2) to quantify seed dispersal kernels and seed deposition patterns generated by bats.

4) To develop a general model for the allometric relations of seed dispersal and to test this model against empirical data.

5) To use the model developed in (4) to assess the performance of Egyptian fruit bats as LDD vectors compared with other frugivorous mammals and birds.

I predicted the bats to be important seed dispersers and to disperse seeds over long distances as found by fruit bats around the world. Because it is a generalist forager, I expected it to be a potential vector for invasive plant species. Because of their active flight ability, fruit bats are expected to disperse seeds over long distances comparable to flying birds and much farther than non-flying mammals and birds.

2. GENERAL METHODOLOGY

Movement of small animals has been measured to date mainly by low resolution sampling in time and space or by indirect measures (Bridge *et al.* 2011). Recent miniaturization and power reduction in GPS technology enabled me, for the first time, to monitor bat movement over relatively large spatial scales in a very high spatiotemporal resolution, and, consequently, to quantify the bats' flight parameters as well as their foraging pattern and navigational skills within a heterogeneous landscape. In addition, the high spatiotemporal resolution enabled modeling and predicting the potential of the bats as seed dispersers, and assessing how the distance from the roost and different landscape elements shape the seed shadow the bats generate.

Study sites:

Egyptian fruit bats (*Rousettus aegyptiacus*) were captured by mist nets at Sgafim cave (31° 40' N; 34° 54' E; Altitude 250 meters above sea level), upon exiting the cave after sunset. Captured bats were removed from the mist net and put in cloth bags until treatment. Each bat was checked for sex and measured for mass, forearm length, approximate age and external parasites. Bats were attached to either a radio telemetry device (models: BD-2, PD-2, PD-2C, Holohil Ltd. Canada) in the case of 26 individuals (8 males, 18 females; 8 juveniles and 18 adults; mass 129.4 ± 28 g; forearm length 90 ± 5.2 mm; mean ± s.d.) or GPS devices with Datalogger attached to 74 individuals of both sexes (48 males, 26 females). For GPS attachment, I used only adult bats with body mass >130 g (mass 142 ± 21g; forearm length 93 ± 4 mm). Experiments were carried out between November 2005 and December 2009; they spanned all seasons, a variety of weather conditions and moon phases.

GPS tracking device and sampling rate:

Bats (N=74) were equipped with a tracking device that included a lightweight GPS data-logger (GiPSy2, TechnoSmArt, Rome, Italy) plus a radio-telemetry unit (BD-2, Holohil Systems, Canada). The average weight of the GPS/telemetry combined pack was 10.8 ± 1.5 g (range 6.9–13.0 g), including batteries, protective casing and attachment to the bat. This weight constituted 7.3% ± 1.2% of the bats' body mass (range 4.0% to 9.6%). The mass limit to add to the bat was selected as 10%, as bats with body mass larger than 70 g do not need to follow the 5% rule of mass (Aldridge & Brigham 1988a). Transmitter load bias was tested by comparing the bats’ flight parameters between the first night and later nights, and between flight distances and recovery rate of heavy load (radio transmitters with GPS and light load transmitters (i.e., radio transmitters only).

The dimensions of the GPS/telemetry pack were 48 mm (length) × 23 mm (width) × 11 mm (height). The miniature GPS trackers consisted of a GPS receiver module (U-blox, Thalwil, Switzerland) plus data-logger (Flash memory) and a quarter-wavelength antenna (47.6 mm length). The GPS devices were modified for tracking bats: Specifically, I modified the devices to allow flexible on/off activation schedules, such that the GPS was active only at night and inactive during the day (when bats were inside the cave). Additionally, in some cases, the GPS was activated for only part of the night; this saved battery power, and allowed GPS-recording of bats' movements for up to 4 consecutive nights. All the bats were also tracked manually by standard radio-telemetry triangulation.

Radio telemetry tracking device and sampling rate:

Bats (N=26) were equipped with a radio telemetry tracking device that included a lightweight radio-telemetry unit (BD-2, PD-2 and PD-2C, Holohil Systems, Canada) attached to either their back between the shoulders (near centre of mass) or as a collar around their neck (model PD-2C). Bats were tracked by 2–4 teams simultaneously, and bat location was determined by triangulation of all tracking teams. Bat location was recorded once every 2 minutes for durations of 2hrs a night to full nights and from 1 to 13 nights.

Device attachment and marking of individual bats:

Prior to attachment, fur was removed by scissors and a shaving razor. Medical skin adhesive (Torbot Liquid Bonding Cement, Torbot Group, RI, USA) was used to attach the Radio telemetry or GPS device to the bat's skin, directly above the center-of-mass of the animal's body at its back. The bat was also marked with a subcutaneous identification tag (UNO Mini-Transponder, Zevenaar, Netherlands) in order to verify that all tracked bats were indeed distinct individuals.

GPS sampling rate and time-extent of data collection:

The mass and size of the GPS battery limited the device's lifetime, and therefore I modified the GPS sampling-rate and activation schedule according to experimental needs, to enable collection of more data. Total time-extent of data collection ranged from full sampling over one night, to collecting 3 hours of data per night over several consecutive nights (up to 4 nights). Sampling rate within GPS sampling ranged from 1 fix a second up to 1 fix every 3 minutes.

Release of the bats:

Prior to release, bats were given a few centiliters of fruit juice, to reduce stress of capture and handling. To eliminate group-navigation by our experimental bats, I (i) released the bats only after all other bats left the cave (for bats released near the cave), and (ii) if several bats were tagged at the same night, I released them individually at > 20 min intervals. Prior to release, bats were rotated multiple times and released to a random direction.

Cave released bats were captured and released at Sgafim cave (31^{o} 40' N; 34^{o} 54' E; altitude, 250 meters above sea level). For homing experiments, I used the same capture and attachment protocol as with cave-release bats. I carried out three sets of homing releases in the Negev Desert, releasing the bats at the following locations: (i)

Gva'ot Goral (aerial distance of 44 km from capture site, 31^{o} 17' N; 34^{o} 49' E; altitude, 419 meters above sea level); (ii) inside HaMakhtesh HaGadol natural erosional crater (aerial distance of 84.5 km from capture site, 30^{o} 55' N; 34^{o} 58' E; altitude, 400 meters above sea level); and (iii) outside of HaMakhtesh HaGadol (aerial distance of 79 km from capture site, 30^{o} 58' N; 34^{o} 58' E; altitude, 638 meters above sea level). Translocation was done by car, driving the bats a total ground-distance of 58, 111 and 105 km, respectively. During the entire transport, bats were held inside cloth bags.

For the release in Gva'ot Goral, upon arrival to the release location, bats were randomly assigned to one of two treatment groups: (i) N=11 bats were released immediately; (ii) N=10 bats were kept in a closed cage for at least 3 hours, given fruit and water ad lib, as well as being fed by hand, and only then released (~3 hours before sunrise). For the inside- and outside-crater releases, bats were held in cloth bags during the drive to the release site, with ad lib food provided; upon arrival to the site, the bats were released using the same protocol.

GPS recovery and data download:

GPS tags with telemetry transmitters were retrieved after they had fallen from the bat to the ground (usual time frame, approximately one to five weeks). Retrieval of the GPS unit was done using the radio-telemetry signal. Data download was possible only by physically retrieving the device. Retrieval rate of GPS devices was 89% and 62% for bats released at the cave and at homing experiments, respectively. In total, I retrieved 54 of the 74 deployed GPS devices (73%).

Movement of bats:

I included only data-points that had high accuracy, by including only individual points that were based on at least 4 satellites and Positional Dilution of Precision (PDOP) < 12. Preliminary testing has shown that such criteria enable optimal data to accuracy ratio

(Mills, Patterson, & Murray 2006) and give a horizontal and vertical accuracy of 3.88 m and 8.74 m for 95% of the locations, respectively. Subcutaneous identification tags verified that all bats were indeed distinct individuals.

Preliminary tests showed that 99% of all locations of non-moving GPS devices showed a speed of below 2.78 m/s, this is due to background noise of satellite reception (Kaplan & Hegarty 2005).

All GPS tracks were allocated to 'flight' or 'quiescent' behavior (where quiescent is defined as resting or sauntering behavior). A ‘flight’ segment was defined as consecutive locations of over 20 seconds where ground speed was greater than 2.78 m/s; all other segments were designated as ‘quiescent’. Despite the high spatial resolution used, it was impossible to distinguish between the ‘quiescent’ behavior of resting bats and bats feeding while moving very short distances. I set a 5 km cut-off point for all flight segments, to distinguish between 'local' and 'commuting flight', where commuting flight segments were defined as a flight segment with a cumulative distance of equal or greater than 5 km, and local flights as a flight segment with an cumulative distance of less than 5 km.

For all flight segments, I computed the following trajectory data: (I) median altitude above ground level (m); (ii) median ground speed (m/s); (iii) total distance traveled (m); (iv) Displacement (m); (v) total duration (minutes) and (vi) straightness index (defined as D/L, where D is the distance of the straight line from the starting point to the goal (beeline distance) and L is the total length of the segment flown).

Flight tracks were considered similar between different nights if the measured perpendicular of one track towards the other was less than one kilometer during the entire track.

Fruit trees:

Trees visited by marked bats were mapped using a handheld GPS (Garmin 12XL, Garmin Inc. USA); the trees were identified to the species level and recorded for fruit fecundity as well as ripeness. For each bat, a 'first tree stop' was defined as the first stop made by the bat at a fruit tree that lasted more than ten minutes. In addition, I surveyed the area from the roost site to the selected tree to find fruit trees of the same species with similar fecundity and ripeness. The tree found closest to the roost of the same species and of similar fecundity to the 'first tree stop' was defined as the ‘nearest tree’. Of all 22 GPS tagged bats, only once was the ‘nearest tree’ the same as the ‘first tree stop’ (4.5% of all cases). In addition, I inspected all quiescent locations of all tracked bats by physically visiting the location and identifying the tree species as well as evaluating its fruiting status.

Of the 22 GPS tagged bats, ten contained movement data for the entire night. For each of those bats, I also calculated the distance from the roost to the tree in which the bat stayed for the longest duration (‘longest visit’), and the distance from the roost to all quiescent stops weighted by the stop duration (‘weighted average distance’).

I created a large dataset of fruit tree distribution, comprising all known locations of the individual fruit trees of all species visited by the bats during the ‘first tree stop’ (defined earlier in this section). In total, the dataset includes 6,386,938 individual trees of 12 different species, most of them common to this region (Tous & Ferguson 1996). This extensive database was comprised from the following sources: (a) GIS data of all fruit plantations in the relevant area (received from the Israeli Fruit Council in Bet Dagan, Ministry of Agriculture 2007); (b) BioGIS–the national database of the flora and fauna of Israel that includes databases such as the Israeli Nature and Parks Authority, Danin flora Database, SPNI–flora database and the Hebrew University Herbarium database; (c) ROTEM–Israel Plant Information Center; (d) KKL-JNF database and (e) my own surveys of fruit trees totaling 32 days in January 2007–December 2009 designated to fill up gaps in the database. A polygon of plantations was converted into point localities by randomly adding point locations within the plantation polygon at an average density of one tree every 16 m^2. For data analysis, I focused only on trees located within a radius of 25 km from the Sgafim roost.

Using the fruit tree database, I estimated a kernel smoothing density, and calculated a one-dimensional cumulative distribution function (CDF) as well as a one-dimensional probability distribution function (PDF). I then calculated for each of the 22 GPS-marked bats, the relative location of the ‘first tree stop’ within the one-dimensional CDF. For the 10 bats with full night sampling data, I also calculated the location of the ‘longest visit’ tree and of the ‘weighted average distance’ for each of the quiescent stops, as explained above.

The attractiveness map:

The fruit tree distribution database was used to construct a raster map of an 50 km by 50 km divided into 2,500 grid cells of 1 km^2 with the Sgafim roost in its center. For each of the grid cells, I calculated two parameters: The number of fruit trees within the cell (to estimate potential gain), and the distance between the center of the cell and the center of the map (to estimate potential cost). I then calculated for each cell an ‘attractiveness score’ by dividing the potential gain by the potential cost (Matthiopoulos 2003). To normalize the attractiveness score, I used the following function: $[X_i\text{-min}(X)] / [\max(X)\text{-min}(X)]$, so the relative scores range between zero and one.

In a landscape with variable attractiveness, simple optimal foraging theory principles (section 1.2) predict that individual bats will prefer cells of higher-than-average attractiveness than would be expected from a random selection of cells. To test this prediction, I first contrasted the overall distribution of attractiveness scores in the entire landscape with the distribution of attractiveness scores of cells selected by individual bats (see section 3.1 for more details).

I then compared the distribution of each of the simulation results with the result of six different datasets: (a) all quiescent and local flights of the 10 bats with full night tracking, (b) all quiescent data of the 10 bats with full night tracking data, (c) The fruit trees the 10 bats visited, (d), (e) and (f) are the same as (a), (b) and (c), respectively, for all the 22 bats I tracked. For reference, I also tested the mean attractiveness of 22 fruit trees located closest to the roost which are of the same species and ripeness state as the 22 fruit trees of the 'first tree stop' selected by the bats.

For these two analyses, I used only grid cells whose center is within a 25 km radius around the Sgafim cave roost, the longest documented foraging movement of an

Egyptian fruit bat in my study (Tsoar *et al.* 2011b) and in other studies as well (Jacobsen & Du Plessis 1976; Makin 1990).

Second, to estimate the statistical significance of the departure of the observed cases from random selection, I performed a Monte-Carlo simulation, in which virtual bats randomly select a grid cells with at least one fruit tree (bats are not expected to forage for food in locations having no fruit trees) and otherwise irrespective of its attractiveness score. This random simulation was carried out 15,000 times for each of the 7 datasets mentioned above, to estimate the probability distribution of the particular number of bats to obtain a certain average attractiveness score.

Gut retention time:

The gut retention time (GRT) of seeds eaten by Egyptian fruit bats was estimated from a set of standard laboratory experiments (Sun *et al.* 1997; Loiselle & Blake 1999; Holbrook & Smith 2000) on 13 individual bats, all taken from a captive colony that was recently captured from the wild and held during this experiment in individual cages. Bats were offered two different fruits, selected to represent common plants dispersed by bat endozoochory (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, URL: www.nature.org). Following a previous empirically-based generalization for frugivores (Murray 1988; Wahaj *et al.* 1998). I fitted a gamma function to the observed distribution of GRT for each of the two fruit species separately, and for all data pooled together.

Dispersal distance kernel:

Bat-generated dispersal distance kernels were calculated by multiplying the probability that the bat was 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). I separated the movement data of the tracked bats into two groups, according to the fruit trees they visited, and calculated 4 dispersal distance kernels from the different GRT distributions:

(a) alien, naturalized and invasive tree species with the pooled GRT distribution; (b) native tree species with the pooled GRT distribution; (c) all trees with the GRT distribution for *F. carica* alone; and (d) all trees with the GRT distribution for *M. alba* alone.

Data analysis:

All data analyses were carried out using Matlab (Matlab 2008a, Mathworks Inc., USA); Tree locations were mapped using a Garmin 12XL GPS (Garmin Ltd. USA) and digitized into ArcMap (ArcMap 9.2, ESRI Inc., USA); Ground elevation was extracted from a digital terrain model (DTM) layer with a cell size of 25 m^2 (Hall, J.K., Geological Survey of Israel, Israel). Statistical tests were undertaken using the SPSS statistical software (SPSS 15, SPSS Inc., USA). All tests were considered significant if $P < 0.05$. If multiple tests were conducted, I used the Dunn-Šidák correction for significance (Abdi 2007).

3. RESULTS

CHAPTER 1

The importance of accurate and detailed quantification of resource distribution and forager movements for understanding animal foraging patterns in heterogeneous landscapes, illustrated by the Egyptian fruit bat

This chapter has not yet been submitted to a peer reviewed journal

The importance of accurate and detailed quantification of resource distribution and forager movements for understanding animal foraging patterns in heterogeneous landscapes, illustrated by the Egyptian fruit bat

Tsoar A[1,*], Nathan R[1]

1 - The Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, The Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel.

** – Current address: Nature and Parks Authority, Ha Avot 19 Beer Sheva, Israel.*

Keywords: *Rousettus aegyptiacus*, optimal foraging, central place forager, flight track, GPS, landscape, fruit trees, frugivore, Chiroptera, attractiveness map

To whom correspondence should be addressed: E-mail: asaf.tsoar@mail.huji.ac.il

Abstract

The distribution of resources plays a key role in determining the movement and distribution of foraging animals in heterogeneous landscapes. Optimal foragers are expected to maximize their food intake in relation to the cost and risk of movement. Central-place foragers should also account for an additional constraint imposed by the need to return to the central place at the end of the foraging bout. We studied the foraging movements of the Egyptian fruit bat (*Rousettus aegyptiacus*) in relation to the spatially explicit distribution of its food resources in a heterogeneous landscape. More specifically, we examined the level of fidelity of the bats to their central place, the factors affecting their flight tracks, and the extent to which the foraging movement correspond to simple predictions of optimal foraging and ideal free distribution theories. By using a spatially explicit empirical model, we also examined the mechanisms by which bats optimize their foraging movement.

Egyptian fruit bats captured when exiting their roosting cave after sunset were equipped with a radio telemetry (N=26) or a GPS (N=22) tracking device. The bats were released near their roost and tracked for up to 11 weeks. The GPS tags provided flight tracks of free-ranging wild bats in an unprecedentedly high spatial and temporal resolution. This has provided the means to compare the spatial foraging patterns of the bats to the corresponding distribution of over 6.3 million fruit trees mapped in the entire foraging landscape.

We found that bats exhibit a distinct foraging pattern of a long, fast, high and straight flight path directly to a specific fruit tree, followed by local foraging nearby, and repeatedly returning to the same tree night after night. Such a foraging pattern was counterintuitive due to the presence of numerous alternative fruit trees with similar ripe fruit closer to the roost. To address this puzzle, we compared several features of the foraging movements of the bats to the spatial variation of site attractiveness, a measure combining the basic gains (fruit trees) and costs (distance from the roost) of foraging at each 1 km^2 cell in the landscape. We found a strong tendency of the bats to select highly attractive sites compared to a random selection of sites. Interestingly, the sites

selected by the bats were significantly more attractive than sites containing the closest fruit trees of the same species and ripeness, illustrating the importance of accounting for movement and resource distribution in a fine-detailed manner. Furthermore, we found that spatial distribution of foraging sites was similar to the distribution of fruit trees in the landscape, in accordance to the simple “null model” predictions of the ideal free distribution theory. We conclude that accurate and detailed quantification of resource distribution can explain seemingly counterintuitive foraging patterns, which are similar to foraging patterns found in other studies of fruit bats, suggesting that fruit bats follow simple optimal foraging principles.

Introduction

A major challenge in ecology is to elucidate the mechanism governing the diversity and distribution of organisms at different spatial and temporal scales (Hooper *et al.* 2005). Foraging is one of the basic and most common daily activities for many, if not most, animals, defined as the act of searching and processing of food or provisions (Stephens & Krebs 1986). Optimal foraging theories such as the marginal value theorem—at the individual level—and the ideal free distribution (IFD)—at the population level—were developed to better understand the foraging patterns of animals and to explain their movements and spatial distribution (MacArthur & Pianka 1966; Fretwell & Lucas 1969; Fretwell 1972; Charnov 1976; Pyke 1984; Stephens & Krebs 1986; Tregenza 1995). These theories basically assert that a forager should maximize the gains (e.g., food intake and mate finding) in relation to the costs (e.g., locomotion cost and predation risk) of foraging in a heterogeneous landscape. Perhaps the simplest formulation of these principles implies that animals should forage at sites that are attractive in terms of the food abundance (potential gain) in relation to travel distance (cost in terms of energetic as well as predation risk) (Stephens & Krebs 1986; Rosenberg & McKelvey 1999; Matthiopoulos 2003).

The movement of a foraging animal might be constrained by external or behavioral restraints such as physical barriers, or the need of the forager to return to its refuge at specific intervals (Rosenberg & McKelvey 1999; Matthiopoulos 2003). A Central place foraging (CPF) strategy is where a forager returns to a specific location, such as a nest or a safe site of reduced exposure to predators (Orians & Pearson 1979; Sih, Petranka, & Kats 1988; Abramsky *et al.* 1990). Central place foragers might differ in their fidelity to the central place (Hamilton *et al.* 1967; Hamilton, Watt, & Annual 1970; Lewis 1995), and the duration and area of their foraging are often limited (Rosenberg & McKelvey 1999; Olsson *et al.* 2008; Rosenberg *et al.* 2011). Thus, all else being equal, site attractiveness generally declines with increasing distance from the central place (Matthiopoulos 2003).

At the population level, the most basic principles of optimal foraging theory have been implemented in the context of the ‘Ideal Free Distribution’ (IFD) theory (Fretwell & Lucas 1969; Fretwell 1972). Assuming that foraging animals have full knowledge of the available resources, make perfect decisions in terms of their net gain (thus, ‘ideal’) and have no travel limitations or costs (thus, ‘free’), IFD theory predicts that foragers will be distributed in a way that equalizes the net gain among individuals, so that the distribution of the foragers would match the distribution of their resources. Although many empirical studies have shown that these assumptions are often violated (see Kennedy & Gray (1993) for a critical review; (Tregenza 1995; Krivan *et al.* 2008), the IDF theory provides a useful starting point or a null model to assess optimality of foraging patterns. The spatial distribution and the temporal availability of fruits vary considerably among plant species in time and space (Condit *et al.* 2000; Hampe 2003). Fruit bats have been found to change their foraging behavior due to changes in the landscape and distance from roost (Cosson *et al.* 1999; Mcdonald-Madden *et al.* 2005; Rainho & Palmeirim 2011; Nakamoto *et al.* 2011).

A challenging basic question in ecology is whether such simple optimal foraging principles can explain observed foraging patterns of free-ranging wild animals in heterogeneous landscapes? This challenge appears insurmountable, given the extreme difficulty of measuring relevant potentially influential factors such as energy income and expenditure, predation risk, cognitive abilities, spatial memory, physiological state and personality, as well as the need to control for intra- and inter-specific competition and for the effects of many other external factors that can impact foragers in a given landscape (Pyke 1984; Olsson *et al.* 2008). We can, however, rephrase the question to ask whether a very simple measure of site attractiveness – food abundance divided by travel distance – can help elucidate optimality of movements and distribution of free-ranging foragers, assuming that other potentially influential factors either correspond to this simple measure or have a minor effect.

Assessing this simple measure of site attractiveness is now feasible for many species due to rapid advances in two complementary methodologies. First, recent miniaturization of Global Positioning System (GPS) tracking devices (Hebblewhite &

Haydon 2010; Robinson *et al.* 2010; Bridge *et al.* 2011) enables accurate quantification of foraging movements of free-ranging animals. Particularly useful are GPS data-loggers that can sample animal movement in high spatial and temporal resolution. This high sampling resolution – still not feasible via radio or satellite telemetry – is often necessary to distinguish the specific resource (e.g. a fruit tree) approached by the foraging animal. Second, tools of Geographical Information Systems (GIS) and the existence of large-scale spatial databases, enable fine detailed mapping of the spatial distribution of environmental features such as food resources. These two components set the stage for elucidating the mechanisms driving the movement of individual free-ranging wild animals (Nathan *et al*. 2008)

In this study, we used cutting-edge GPS technology and GIS tools to quantify foraging movements of Egyptian fruit bats (*Rousettus aegyptiacus*) and the spatially explicit distribution of their food resources in a typical heterogeneous Mediterranean landscape. Frugivorous bats are common in most continents of the world and are known to be important dispersers of plant seeds (Kalko *et al.* 1996; Shilton *et al.* 1999; Shanahan & Compton 2001; Muscarella & Fleming 2007; Jones *et al.* 2009; Tsoar *et al.* 2011b; Kunz *et al.* 2011). Most bats exhibit high roost fidelity explained by the relative rarity of their roosts (Lewis 1995). Lewis (see also Kunz & Lumsden (2003)) defined roost fidelity as a change in roost location less than once every 10 days, or occupancy of a primary roost more than 70% of the time (Lewis 1995).

Previous studies of foraging patterns of fruit bats found a tendency of individual bats to return not only to the same roost but also to the same fruit tree and in some cases by the same flight route. Short-tailed fruit bats (*Carollia perspicillata*) studied in Costa Rica were found to disregard new as well as nearby food patches while commuting to a specific foraging tree night after night (Fleming, Heithaus, & Sawyer 1977; Heithaus *et al.* 1978; Fleming & Heithaus 1986). High fidelity to specific fruit trees, despite availability of similar trees closer to the roost, were documented also for the fruit bats *Artibeus jamaicensis* (Morrison 1978a). A similar pattern was found in some of the Old World fruit bats of the Pteropodidae family; *Eidolon helvum* was found to "*fly well beyond the most immediate food sources when foraging*" (Richter & Cumming 2005, p.

35). Andrianaivoarivelo et al. (2011) found *Rousettus madagascariensis* to fly repeatedly and in straight routes of at least 8 km from roost to foraging site. A repeated flight track was also found in *Rousettus leschenaultia* (Tang *et al.* 2010).

The high fidelity of fruit bats to specific trees necessitates high fruiting predictability and long ripeness duration of fruit trees as prerequisites (Chapman *et al.* 1999). In the Eastern Mediterranean region, fruit trees bloom on consistent dates, have predictable fecundity, and ripe fruit can be found on the tree for relatively long durations. Carobs (*Ceratonia siliqua*), for example, can be found ripe on the tree all year round (A.T. personal observations; Izhaki et al., 1995; Korine et al., 1998). Potential qualitative evidence for tree fidelity in Egyptian fruit bats is provided by Makin (1990), reporting a tendency of bats to be recaptured near the fruit tree where first caught.

As in all flying animals, bats can minimize their flight energy expenditure per distance (maximal range speed, V_{mr}) or per time (minimal power speed, V_{mp}) (Norberg & Rayner 1987; Pennycuick 1989; Rayner 1999). Optimal flight theory predicts that foraging animals will fly at their V_{mp} (minimizing the energy per time) while commuting animals are predicted to fly at V_{mr} (minimizing the flight cost per distance traveled). Such modeling predictions do not take into consideration other factors, and in fact bats have been shown to change their flight speed according to environmental conditions, aerial feeding, and even due to perceived predation risk (Winter 1999; Holderied & Jones 2009; Grodzinski *et al.* 2009). The optimal flight model predicts Egyptian fruit bats to fly at optimal flight speeds of $V_{mp} = 9.2$ m/s; $V_{mr} = 15.8$ m/s (calculated by the software ‘Flight’ version 1.23; (Pennycuick 2008)). While the optimal flight model created by Norberg & Rayner (1987) predicted flight speeds of $V_{mp} = 4.59$ m/s; $V_{mr} = 6.91$ m/s (calculated as explained in Grodzinski *et al.* 2009). Previous flight measurements on free ranging Egyptian fruit bats estimated lower flight speeds of commuting flight speed at 15–25 km/h (Jacobsen *et al.* 1986). Any deviation from the optimal flight theory predictions is expected to be due to additional considerations (Holderied & Jones 2009).

My goal is to examine whether the Egyptian fruit bat optimizes its foraging behavior. Is the bat's movement pattern within the landscape optimized in some way? Do bats optimize their foraging flight or site? More specifically, my objectives are:

1) To measure the nightly foraging movements of individuals in high spatial and temporal resolution and to assess the level of fidelity of the bats to their roosts and to specific food resources.

2) To map the distribution of the food resources (fruit trees) at the individual tree level across the entire relevant area.

3) To test if the spatial distribution of foraging bats matches the spatial distribution of the resources within the landscape as predicted by the IFD theory.

4) Assuming that (1) will provide evidence for CPF, to use the data obtained in (2) to assess the spatially explicit variation in resource attractiveness in terms of gain (food) versus costs (distance from the roost).

5) To compare several features of bat foraging movements including foraging flights, stops and fruit trees they visited (available from (1)), against the corresponding expectations derived from the attractiveness maps (from (4)).

We predict the Egyptian fruit bat to act as a central place forager, showing high roost fidelity, as expected of cave-roosting bats (Lewis 1995). Because fruit is spatially and temporally predictable within the Eastern Mediterranean landscape, we predict the bats will show high fidelity also to specific foraging areas, as long as the trees have sufficient fruit on them (Morrison 1978a; Fleming 1988; Eby 1991; Parry-Jones & Augee 2001; Vardon *et al.* 2001). We thus predict the bats to fly directly to specific fruit trees. We expect, like other study cases, a direct flight path that will be repeated on consecutive foraging events (Morrison 1978a; Fleming 1988; Andrianaivoarivelo *et al.* 2008) and by flight speed as predicted by optimal flight model at V_{mr}. We expect, based on optimal foraging theory, the bats to forage at sites where the resource attractiveness is higher than average. At the population level, we predict that foraging bats will be distributed in a pattern similar to the density of fruit trees in the landscape, based on the IDF theory.

Materials and Methods

Movement of small animals has been measured to date mainly by low resolution sampling in time and space or by indirect measures (Bridge *et al.* 2011). Recent miniaturization and power reduction in GPS technology enabled me, for the first time, to monitor bat movement over relatively large spatial scales in very high spatiotemporal resolution, and consequently, to quantify bat flight parameters as well as their foraging pattern and navigational skills within a heterogeneous landscape. In addition, the high spatiotemporal resolution enables modeling and predicting the potential of the bats as seed dispersers, and the assessment of how the distance from the roost and different landscape elements shape the seed shadow the bats generate.

Bat capture and study site:

Egyptian fruit bats (*Rousettus aegyptiacus*) were captured by mist nets at Sgafim cave (31° 40' N; 34° 54' E; Altitude 250 meters above sea level; see figure 1), upon exiting the cave after sunset. Captured bats were removed from the mist net and put in cloth bags until treatment. Each bat was checked for sex and measured for, mass, forearm length, approximate age and external parasites. Altogether, 52 bats were marked for this research, 30 males and 22 females. Bats were attached with either a radio telemetry device (models: BD-2, PD-2, PD-2C, Holohil Ltd. Canada), attached to 24 bats, or GPS devices with Datalogger, attached to 28 individuals. Experiments were carried out between November 2005 and May 2009; they spanned all seasons, a variety of weather conditions and moon phases.

GPS tracking device and sampling rate:

Bats (N=28) were equipped with a tracking device that included a lightweight GPS data-logger (GiPSy2, TechnoSmArt, Rome, Italy) plus a radio-telemetry unit (BD-2, Holohil Systems, Canada). With the GPS attachment, we used only adult bats with body mass >130 g (mass 142 ± 21 g; forearm length 93 ± 4 mm). The average weight of the GPS/telemetry combined pack was 10.8 ± 1.5 g (range 6.9–13.0 g), including batteries, protective casing and attachment to the bat. This weight constituted 7.3% ± 1.2% of the bats' body mass (range 4.0% to 9.6%). The mass limit to add to the bat was selected as 10%, as bats with body mass larger than 70 g do not need to follow the 5% rule of mass limit (Aldridge & Brigham 1988b). Transmitter load bias was tested by comparing flight distances and recovery rate of heavy load (radio transmitters with GPS) and light load (radio transmitters only) transmitters.

The dimensions of the GPS/telemetry pack were 48 mm (length) × 23 mm (width) × 11 mm (height). The miniature GPS trackers consisted of a GPS receiver module (U-blox, Thalwil, Switzerland) plus data-logger (Flash memory) and a quarter-wavelength antenna (47.6 mm length). The GPS devices were modified for tracking bats: Specifically, we modified the devices to allow flexible on/off activation schedules, such that the GPS was active only at night and inactive during the day (when bats were inside the cave). Additionally, in some cases, the GPS was activated for only part of the night; that saved battery power, and allowed GPS-recording of bats' movements for up to 4 consecutive nights. All the bats were also tracked manually by standard radio-telemetry triangulation.

Radio telemetry tracking device and sampling rate:

Bats (N=24) were equipped with a radio telemetry tracking device that included a lightweight radio-telemetry unit (BD-2, PD-2 and PD-2C, Holohil Systems, Canada) Bats were tracked by 2–4 teams simultaneously, and bat location was determined by triangulation of all tracking teams. Bat location was recorded once every 2 minutes for durations of from 2 hrs a night to full nights and from 1 to 13 nights.

Device attachment and marking of individual bats:

Prior to attachment, fur was removed by scissors and a shaving razor. Medical skin adhesive (Torbot Liquid Bonding Cement, Torbot Group, RI, USA) was used to attach the radio telemetry or GPS device to the bat's skin, either on their back between the shoulders (near center of mass) or as a collar around their neck (model PD-2C). The bat was also marked with a subcutaneous identification tag (UNO Mini-Transponder, Zevenaar, Netherlands) in order to verify that all tracked bats were indeed distinct individuals.

GPS sampling rate and time-extent of data collection:

The mass and size of the GPS battery limited the device's lifetime, and therefore we modified the GPS sampling-rate and activation schedule according to experimental needs, to enable the collection of more data. Total time-extent of data collection ranged from full sampling over one night, to collecting 3 hours of data per night over several consecutive nights (up to 4 nights). Sampling rate within GPS sampling ranged from 1 fix a second up to 1 fix every 3 minutes.

Bat release:

Bats were released 20 meters from the Sgafim cave entrance. Prior to release, bats were given a few centiliters of fruit juice, to reduce stress of capture and handling. To eliminate group-navigation by our experimental bats, we (i) released the bats only after all other bats left the cave, and (ii) if several bats were tagged on the same night, we released them individually at > 20-min intervals. Prior to release, bats were rotated multiple times and released to a random direction.

GPS recovery and data download:

GPS tags with telemetry transmitters were retrieved after they had fallen from the bat to the ground (fallen from the bat, one to five weeks). Retrieval of the GPS unit was carried out using the radio-telemetry signal. Data download was possible only by physically retrieving the device. Retrieval rate of GPS devices was 89%.

Movement of bats:

Of the GPS data downloaded from the relocated devices, we included only data-points that had high accuracy by including only individual points that were based on at least 4 satellites and Positional Dilution of Precision (PDOP) < 12. Preliminary testing has shown that such criteria enable optimal data to accuracy ratio (Mills *et al.* 2006) and give a horizontal and vertical accuracy of 3.88 m and 8.74 m for 95% of the locations, respectively.

Preliminary tests showed that 99% of all locations of non-moving GPS devices showed a speed of below 2.78 m/s, this is due to background noise of satellite reception (Kaplan & Hegarty 2005).

All GPS tracks were allocated to 'flight' or 'quiescent' behavior (where quiescent is defined as non-moving or sauntering behavior). A ‘flight’ segment was defined as consecutive locations of over 20 seconds where ground speed was greater than 10 km/hr; all other segments were designated as ‘quiescent’. Despite the high spatial resolution used, it was impossible to distinguish within the ‘quiescent’ behavior between resting bats and bats feeding while moving very short distances.

We set a 5 km cutoff point for all flight segments, to distinguish between 'local' and 'commuting flight', where commuting flight segments were defined as a flight segment with a cumulative distance of equal or greater than 5 km, and local flights as a flight segment with an cumulative distance of less than 5 km.

For all flight segments, we computed the following trajectory data: (i) median altitude above ground level (m); (ii) median ground speed (km/hr); (iii) total distance traveled (m); (iv) displacement (m); (v) total duration (minutes) and (vi) straightness index (defined as D/L, where D is the distance of the straight line from the starting point to the goal (beeline distance) and L is the total length of the segment flown).

Flight tracks were considered similar between different nights if the measured perpendicular of one track towards the other was less than one kilometer during the entire track.

Fruit trees:

Trees visited by marked bats were mapped using a handheld GPS (Garmin 12XL, Garmin Inc. USA); the trees were identified to the species level and recorded for fruit fecundity as well as ripeness. For each bat, a 'first tree stop' was defined as the first stop made by the bat at a fruit tree that lasted more than ten minutes. In addition, we surveyed the area from the roost site to the selected tree to find fruit trees of the same species with similar fecundity and ripeness. The tree found closest to the roost of the same species and of similar fecundity to the 'first tree stop' was defined as the ‘nearest tree’. Of all 22 GPS tagged bats, only once was the ‘nearest tree’ the same as the ‘first tree stop’ (4.5% of all cases). In addition, we inspected all quiescent locations of all tracked bats by physically visiting the location and identifying the tree species as well as evaluating its fruiting status.

Of the 22 GPS tagged bats, ten contained movement data for the entire night. For each of those bats, we also calculated the distance from the roost to the tree in which the bat stayed for the longest duration (‘longest visit’), and the distance from the roost to all quiescent stops weighted by the stop duration (‘weighted average distance’).

We created a large dataset of fruit tree distribution, comprising all known locations of individual fruit trees of all species visited by the bats during the ‘first tree stop’ (defined earlier in this section). In total, the dataset includes 6,386,938 individual trees of 12 different species, most of them common to the region (Danin A. personal communication). This extensive database was comprised from the following sources:
(a) GIS data of all fruit plantations in the relevant area (received from the Israeli Fruit

Council in Bet Dagan, Ministry of Agriculture 2007); (b) BioGIS–the national database of the flora and fauna of Israel that includes databases such as the Israeli Nature and Parks Authority, Danin flora Database, SPNI–flora database and the Hebrew University Herbarium database; (c) ROTEM–Israel Plant Information Center; (d) KKL-JNF database and (e) my own surveys of fruit trees totaling 32 days in January 2007 – December 2009 designed to fill gaps in the database. A polygon of plantations was converted into point localities by randomly adding point locations within the plantation polygon at an average density of one tree every 16 m^2. For data analysis, we focused only on trees located within a radius of 25 km from the Sgafim roost.

Using the fruit tree database, we estimated a kernel smoothing density, and calculated a one-dimensional cumulative distribution function (CDF) as well as a one-dimensional probability distribution function (PDF). We then calculated for each of the 22 GPS-marked bats, the relative location of the ‘first tree stop’ within the one-dimensional CDF. For the 10 bats with full night sampling data, we also calculated the location of the ‘longest visit’ tree and the ‘weighted average distance’ for each of the quiescent stops, as explained above.

The attractiveness map:

The fruit tree distribution database was used to construct a raster map of 50 km by 50 km divided into 2,500 grid cells of 1 km^2 with “Sgafim” roost in its center. For each of the grid cells, we calculated two parameters: The number of fruit trees within the cell (to estimate potential gain), and the distance between the center of the cell and the center of the map (to estimate potential cost). We then calculated for each cell an ‘attractiveness score’ by dividing the potential gain by the potential cost (Matthiopoulos 2003). To normalize the attractiveness score, we used the following function:

Normalized score = $[X_i - \min(X)] / [\max(X) - \min(X)]$,

so the relative scores range between zero and one.

Optimal foragers are expected to prefer cells of higher-than-average attractiveness than would be expected from a random selection of cells. To test this prediction, we contrasted the random selection of cells with the distribution of attractiveness scores of cells containing bat selected locations. We compared the distribution of the overall distribution of attractiveness scores in the entire landscape with the result of six different datasets of bat selected locations: (a) all quiescent and local flights of the 10 bats with full night tracking, (b) all quiescent data of the 10 bats with full night tracking data, (c) the fruit trees the 10 bats visited, (d), (e) and (f) are the same as (a), (b) and (c), respectively, carried out for all of the 22 bats we tracked. For reference, we also tested the mean attractiveness of 22 fruit trees located closest to the roost which are of the same species and ripeness state as the 22 fruit trees of the 'first tree stop' selected by the bats.

For these two analyses, we used only grid cells whose center is within a 25 km radius of the Sgafim cave roost, the longest documented foraging movement of an Egyptian fruit bat reported in this study (Tsoar *et al.* 2011b) and in other studies as well (Jacobsen & Du Plessis 1976; Makin 1990).

Second, to estimate the statistical significance of the departure of the observed cases from random selection, we performed a Monte-Carlo simulation, in which virtual bats randomly select grid cells with at least one fruit tree (bats are not expected to forage for food in locations having no fruit trees) and otherwise irrespective of its attractiveness score. This random simulation was carried out 15,000 times; for each of the runs, the mean attractiveness score was calculated. We then compared the mean of each of the 7 datasets mentioned above to the distribution of the random simulation, to estimate the probability distribution of the particular number of bats to obtain a certain average attractiveness score.

Data analysis:

All data analysis were done using Matlab (Matlab 2008a, Mathworks Inc., USA); Tree locations were mapped using a Garmin 12XL GPS (Garmin Ltd. USA) and digitized into ArcMap (ArcMap 9.2, ESRI Inc., USA); Ground elevation was extracted from a digital terrain model (DTM) layer with a cell size of 25 m^2 (Hall, J.K., Geological Survey of Israel, Israel). Statistical tests were done using the SPSS statistical software

(SPSS 15, SPSS Inc., USA). All tests were considered significant if $P < 0.05$. If multiple tests were conducted, we used the Dunn-Šidák correction for significance (Abdi 2007).

Results

Tag recovery and roost fidelity:

We retrieved the vast majority (95%) of GPS tags within 35 days of release. Roost fidelity, calculated by the normal approximation of the binomial distribution for the probability of a marked bat to be found at a random visit to the roost within 35 days of marking, was 0.58 (with a 95% confidence interval of 0.55–0.62). Roost switching, calculated as the probability of a change in the absence or presence of a bat between consecutive visits to the roost, was 0.13 (a 95% confidence interval of 0.1–0.16). On average, bats switched between the Sgafim and other roosts once every 7 days.

Bat foraging tracks and tree fidelity:

All bat tracks were divided into segments relating to one of three behavioral phases: quiescent, local flight or commuting flight. After the removal of partial segments, we got 533 complete segments, comprising 235 'local flight', 24 'commuting flight', and 274 segments defined as 'quiescent' (table 1; figure 2). The total analysis consisted of over 126 hours of high resolution tracking of bats and over 313,000 GPS location points of high accuracy (after filtering out low accuracy data). Neither night enumeration, sex nor area of foraging was significantly different for any of the flight parameters (Kruskal-Wallis test). Similar results were found by Barclay and Jacobs (2011).

Bat tracks were found to have a repeatable pattern in which a bat typically leaves the cave and makes a long, high, and straight flight to distant fruit trees (table 1; figure 2). Once arriving at the selected tree, bats typically foraged on adjacent trees during the entire night. Towards the end of the night, they returned to the cave in a similar long, high, and straight flight (figure 2 and 4(a), blue line). The median distance between fruit trees on which bats stopped was 420 meters. The median convex hull of the foraging sites per bat was 0.052 km^2 (Tsoar *et al.* 2011b).

Repeated commuting flight tracks were collected for six individual bats, of which five showed a repeated flight track between nights (see examples in figure 4). These bats returned to the same fruit-tree up to four consecutive nights. Of the 38 bats for which we collected foraging data, 33 bats were monitored for more than one night. Thirty-two (97%) of them returned to the same tree for at least two nights within the first three nights from release. Moreover, radio-telemetry tracking of 16 additional fruit bats from the same colony showed that bats foraged on the same tree for up to four months (Tsoar *et al.* 2011a).

Most of our GPS tracked bats (90%) started and ended their nightly foraging session with a commuting phase (defined here as a continuous flight for more than 5 km) of fast (median speed, 9.28 m/s), high (median height above the ground, 103.8 meters), straight (median straightness index, 0.92) and long (mean displacement distance of 13,019 meters) flight (Table 2).

The fast flight speed of the bats' commuting flight was found to be similar to the predicted speed for minimum energy by the flight energetic model for Egyptian fruit bats (the model predicted a minimum energy flight speed of 9.2 m/s; calculated by the software 'Flight' version 1.23; (Pennycuick 2008). A different flight model constructed by Norberg and Rayner (1987) predicted a minimum energy flight of 4.59 m/s).

Fruit tree distribution within the landscape:

As expected, bats foraged on natural and cultivated plants as well as on invasive species, feeding on a wide range of fruits, confirming that the Egyptian fruit bat is indeed a generalist frugivore (Izhaki *et al.* 1995; Korine *et al.* 1998, 1999; Kwiecinski & Griffiths 1999; Tsoar *et al.* 2011b).

The spatial distribution of fruit trees within the landscape clearly showed a patchy distribution in which most trees were concentrated north to north-west of the roost (Figure 5), with two distinct concentrations of trees relative to the roost. One was close to the roost (1.5–10 km from roost) and the other further away (11–25 km from roost);

the majority of fruit trees are located 11 km and further from the roost (figure 6).

Fruit trees selected by the foraging bats:

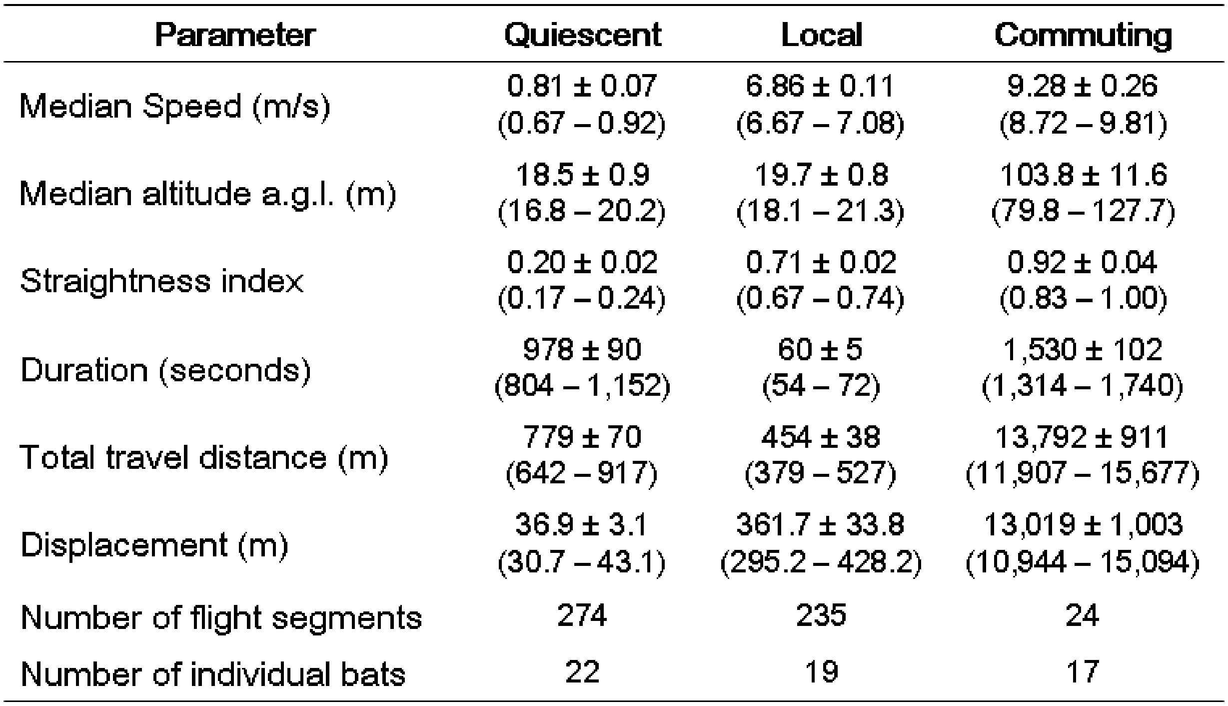
All different measures of the location of trees visited by the bats ('first tree stop', 'longest visit' and 'weighted average distance') were significantly closer to the roost compared with the mean location of all 6,386,938 trees in the relevant area (table 2). In all but one case, the 'first tree stop', was farther from the roost compared with the 'nearest tree' of the same species and ripeness for each of the fruit species (figure 3).

Attractiveness map:

All six Monte-Carlo simulation tests carried out on different selections of the bats' foraging sites, showed bats select cells of high attractiveness (figure 7) more frequently than would be expected by chance (table 3 and figures 8 & 9). Interestingly, the 22 'nearest trees' located at the shortest distance from the roost were on average located in sites of a significantly lower mean attractiveness score than that of the trees selected by the bats. Furthermore, the mean attractiveness score of these 'nearest trees' was not significantly different from the mean score of a randomly selected set of cells of the same sample size (Table 3).

Figure 1: A map of the study area (Google Earth™ background imagery). The red rectangle marks the foraging area of the GPS tracked bats.

Table 1: Summary statistics (mean ± standard error) of different characteristics of the GPS flight tracks of bats for each of the three behavioral phases (quiescent, local flight and commuting flight) for all sampled nights. The 95% confidence interval is given in parentheses. A multiple post-hoc test (Mann-Whitney U-test) with the Dunn-Šidák correction was conducted on the data (α ≤ 0.017), where average was calculated for each parameter per individual bat. All groups were significantly different except two: altitude and total travel distance between local and quiescent flights.



Parameter	Quiescent	Local	Commuting
Median Speed (m/s)	0.81 ± 0.07 (0.67 – 0.92)	6.86 ± 0.11 (6.67 – 7.08)	9.28 ± 0.26 (8.72 – 9.81)
Median altitude a.g.l. (m)	18.5 ± 0.9 (16.8 – 20.2)	19.7 ± 0.8 (18.1 – 21.3)	103.8 ± 11.6 (79.8 – 127.7)
Straightness index	0.20 ± 0.02 (0.17 – 0.24)	0.71 ± 0.02 (0.67 – 0.74)	0.92 ± 0.04 (0.83 – 1.00)
Duration (seconds)	978 ± 90 (804 – 1,152)	60 ± 5 (54 – 72)	1,530 ± 102 (1,314 – 1,740)
Total travel distance (m)	779 ± 70 (642 – 917)	454 ± 38 (379 – 527)	13,792 ± 911 (11,907 – 15,677)
Displacement (m)	36.9 ± 3.1 (30.7 – 43.1)	361.7 ± 33.8 (295.2 – 428.2)	13,019 ± 1,003 (10,944 – 15,094)
Number of flight segments	274	235	24
Number of individual bats	22	19	17

Figure 2: Flight tracks of bats divided by behavioral phases. (**a**) Flight tracks of all 22 foraging bats. Behavioral phases are distinguished by colors: Commuting flight (red), Local flight (green) and Quiescent (black). The green triangle represents the Sgafim roost. (**b**) The relationship between duration and displacement for flight segments for the three behavioral phases of all 22 foraging bats

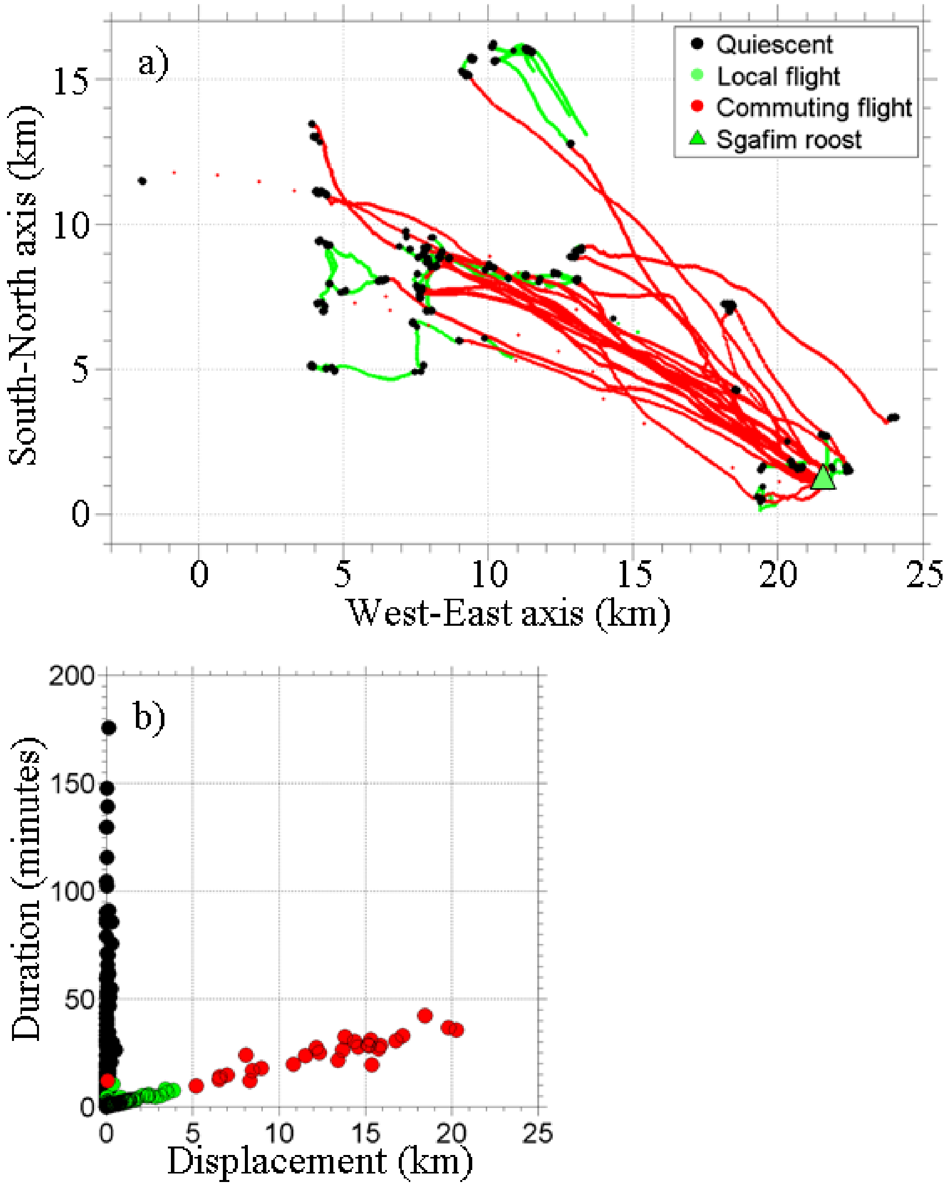


Figure 3: A paired comparison of distance from the roost to the First Tree Stop and to the Nearest Fruit Tree of the same species and ripeness for each of the 22 tracked bats.

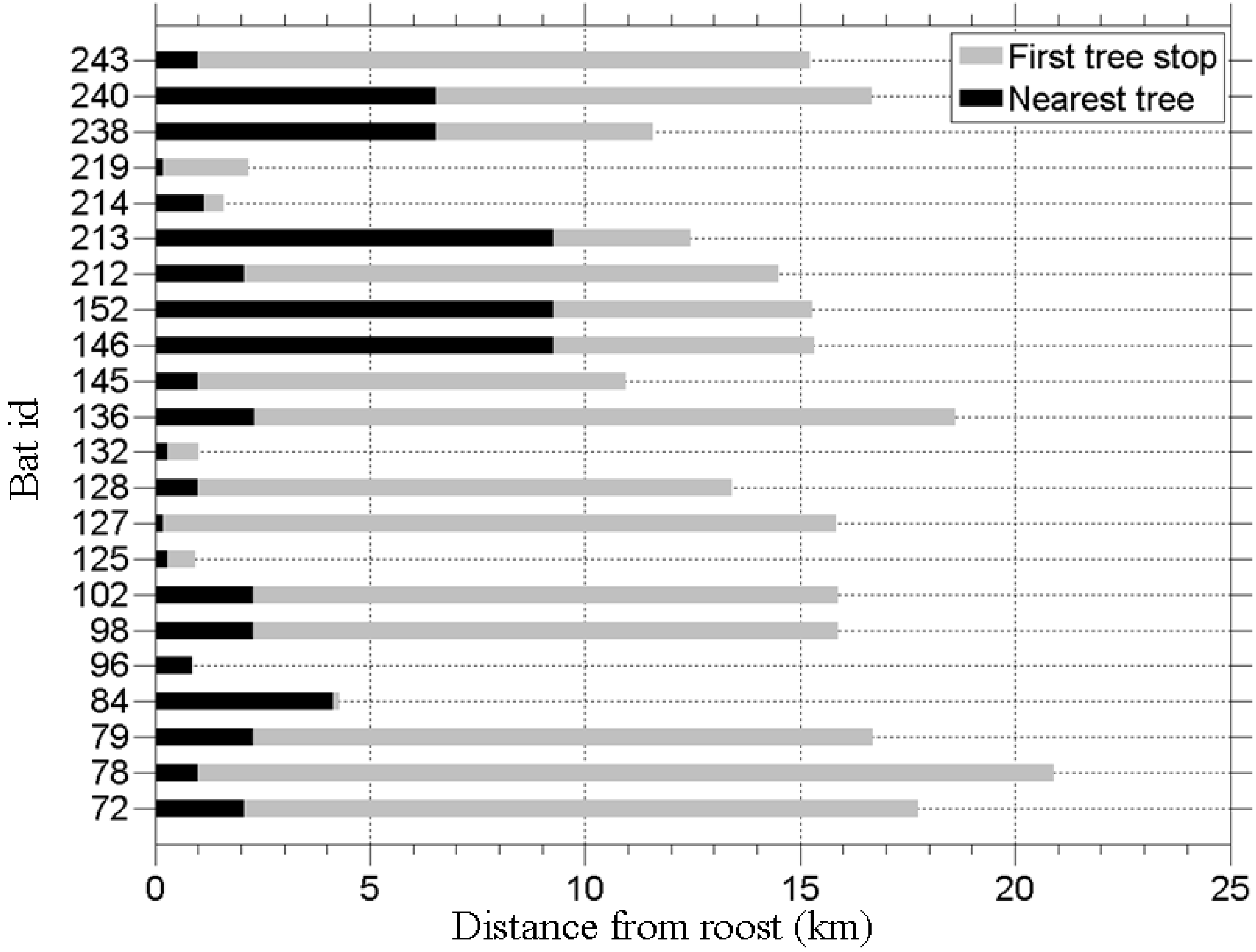


Figure 4: Bat flight tracks superimposed on Google Earth™ background imagery. Lines of different colors represent the flight track of the same bat in different nights (blue, red, green and white stand for the first, second, third and fourth night, respectively). The green triangle portrays the location of Sgafim roost. (a) Bat #243 flying at a similar route on two consecutive nights. (b) Bat #145 flying at two different flight routes to the same foraging site. (c) Foraging site of bat #213 visiting similar fruit trees by a similar route on four consecutive nights. (d) Foraging site of bat #214 visiting the same fruit trees by the same route on three consecutive nights.

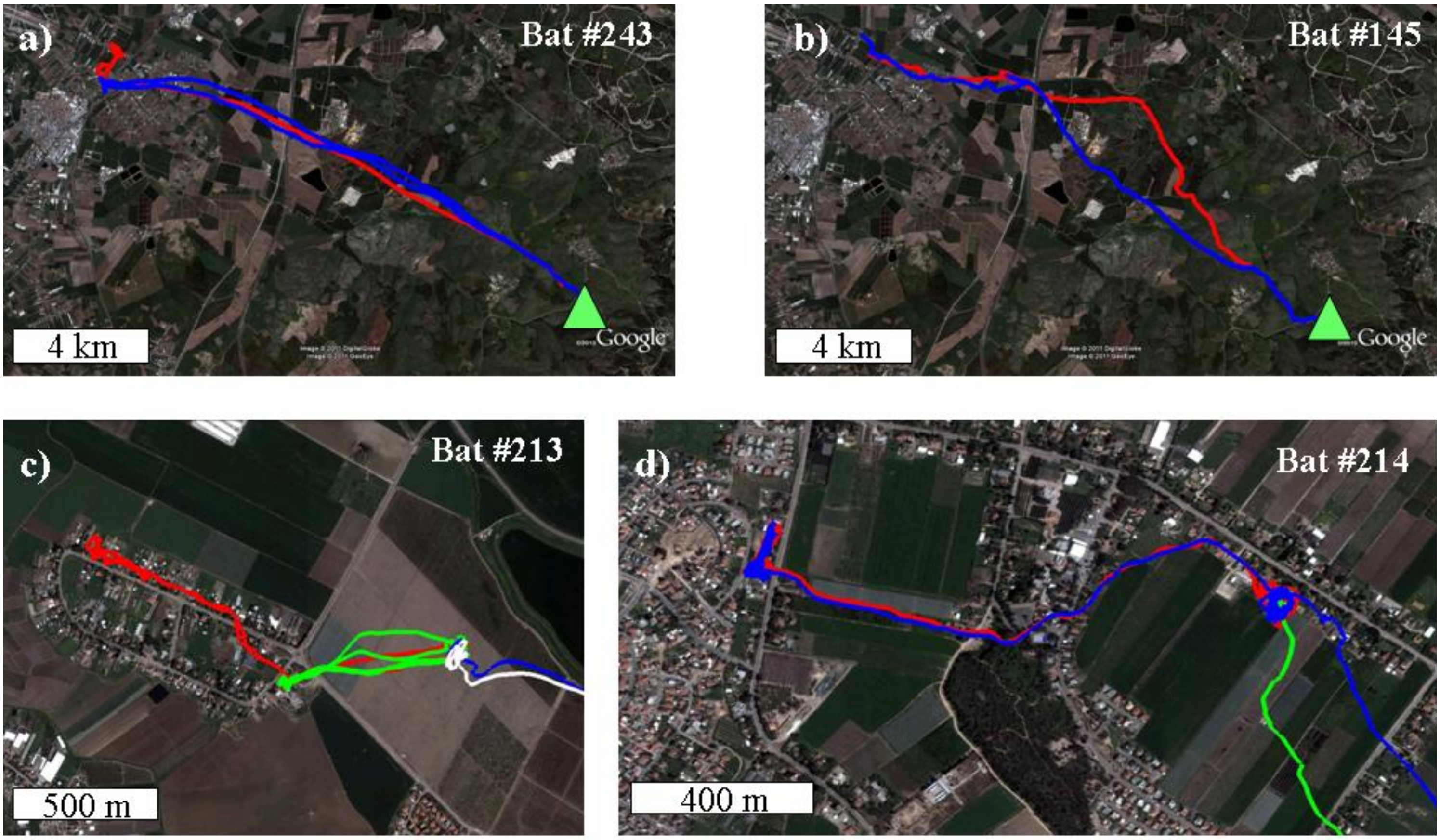


Figure 5: The distribution of fruit trees in relation to the main roost (green triangle) and assessment of site attractiveness. (**a**) A map location of all fruit trees (black dots). The circle marks a radius of 25km around the roost. (**b**) The probability density function of the distance of each fruit tree from the roost. Most trees are located 11-25 km from the roost, with small peaks at approximately 3-4 km and 7-8 km. (**c**) A normalized tree density map in grid cells of 1 km^2 based on (a). (**d**) The normalized attractiveness (tree density divided by the distance from the roost) map. Note the relative high attractiveness of cells close to the roost despite relatively low tree density.

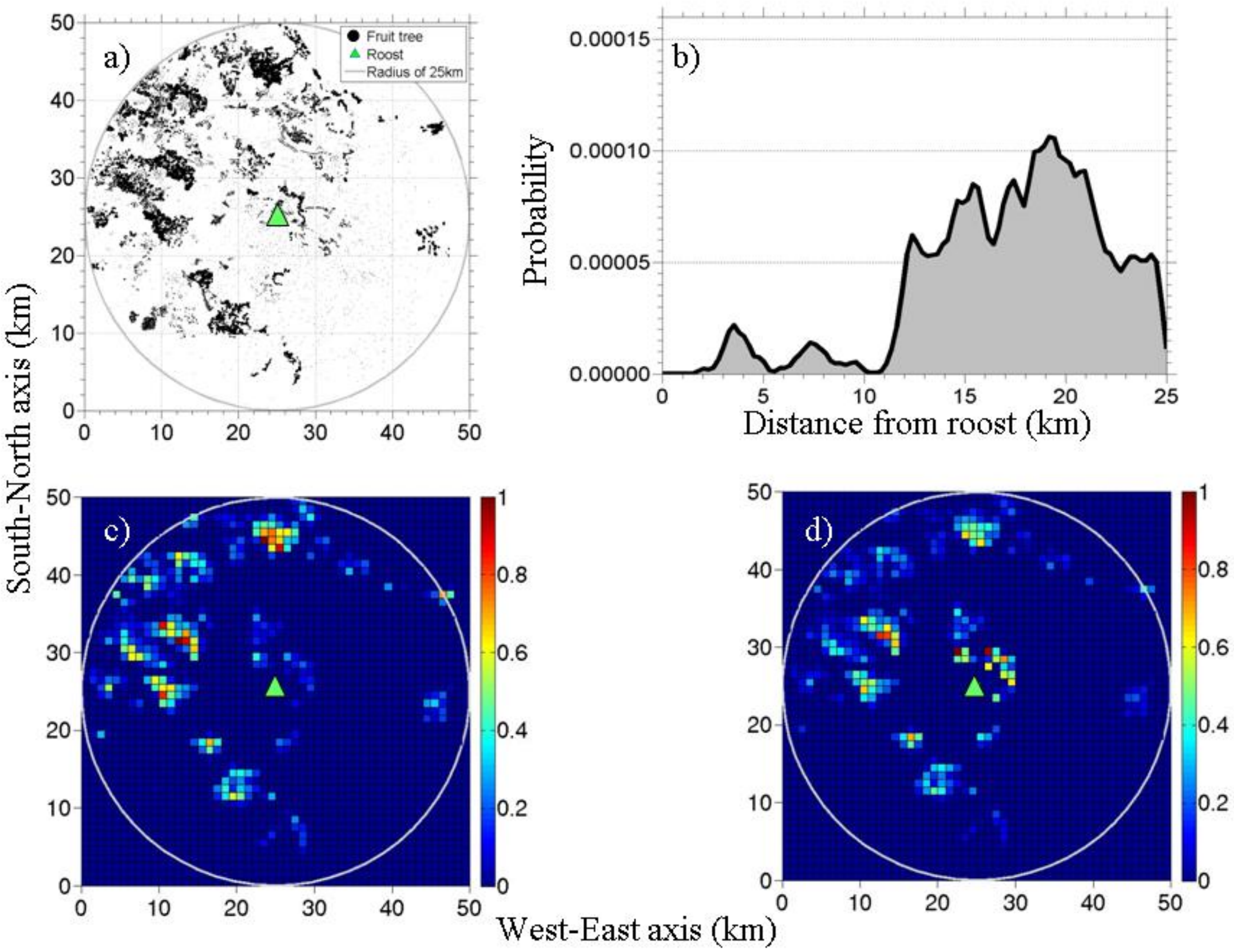
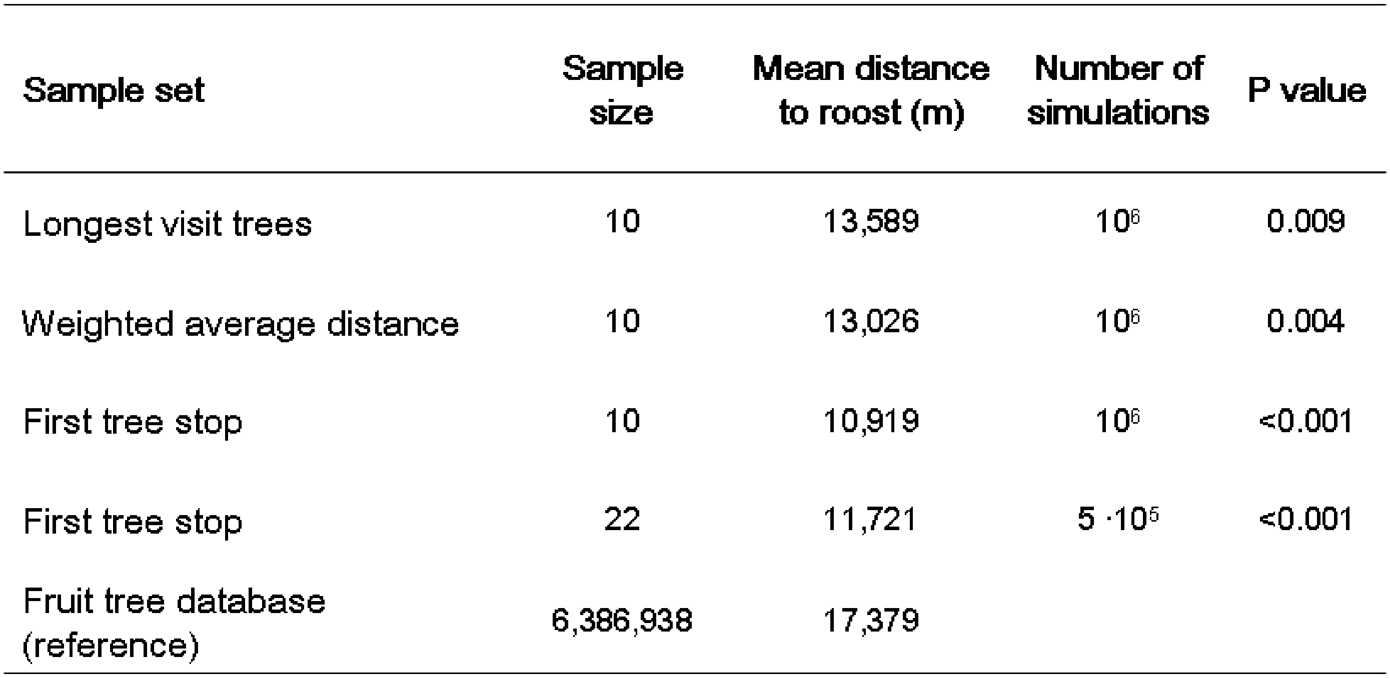


Table 2: Statistics of distance to roost of bat selected fruit trees from several datasets with probability calculated by Monte Carlo simulations. Mean distance to roost was calculated for each of the sample sets (Longest visit trees, weighted average distance, first tree stop for 10 full night bats and first tree stop for all 22 foraging bats). Each sample set was then contrasted to the distribution of the means of a simulation runs for virtual bats of the same group size as the sample set. Simulations were conducted on four data sets: Longest visited tree, weighted average distance, first tree stop of all 22 bats and first tree stop of 10 full night tracked bats. Probability was calculated from the simulation runs of the virtual bat groups for each of the relevant groups. For comparison the bottom row presents the mean distance of all fruit trees in the database.



Sample set	Sample size	Mean distance to roost (m)	Number of simulations	P value
Longest visit trees	10	13,589	10^6	0.009
Weighted average distance	10	13,026	10^6	0.004
First tree stop	10	10,919	10^6	<0.001
First tree stop	22	11,721	$5 \cdot 10^5$	<0.001
Fruit tree database (reference)	6,386,938	17,379		

Figure 6: A truncated probability density function (PDF) of the distance of a fruit tree of up to 25 km from the main roost. The gray shadow line is the PDF for all fruit trees in the database. Also shown are the corresponding smoothed PFDs of the First Tree Stop (red), the Weighted Average Distance (cyan) and Longest Visit (green) calculated for the ten bats with full night tracking.

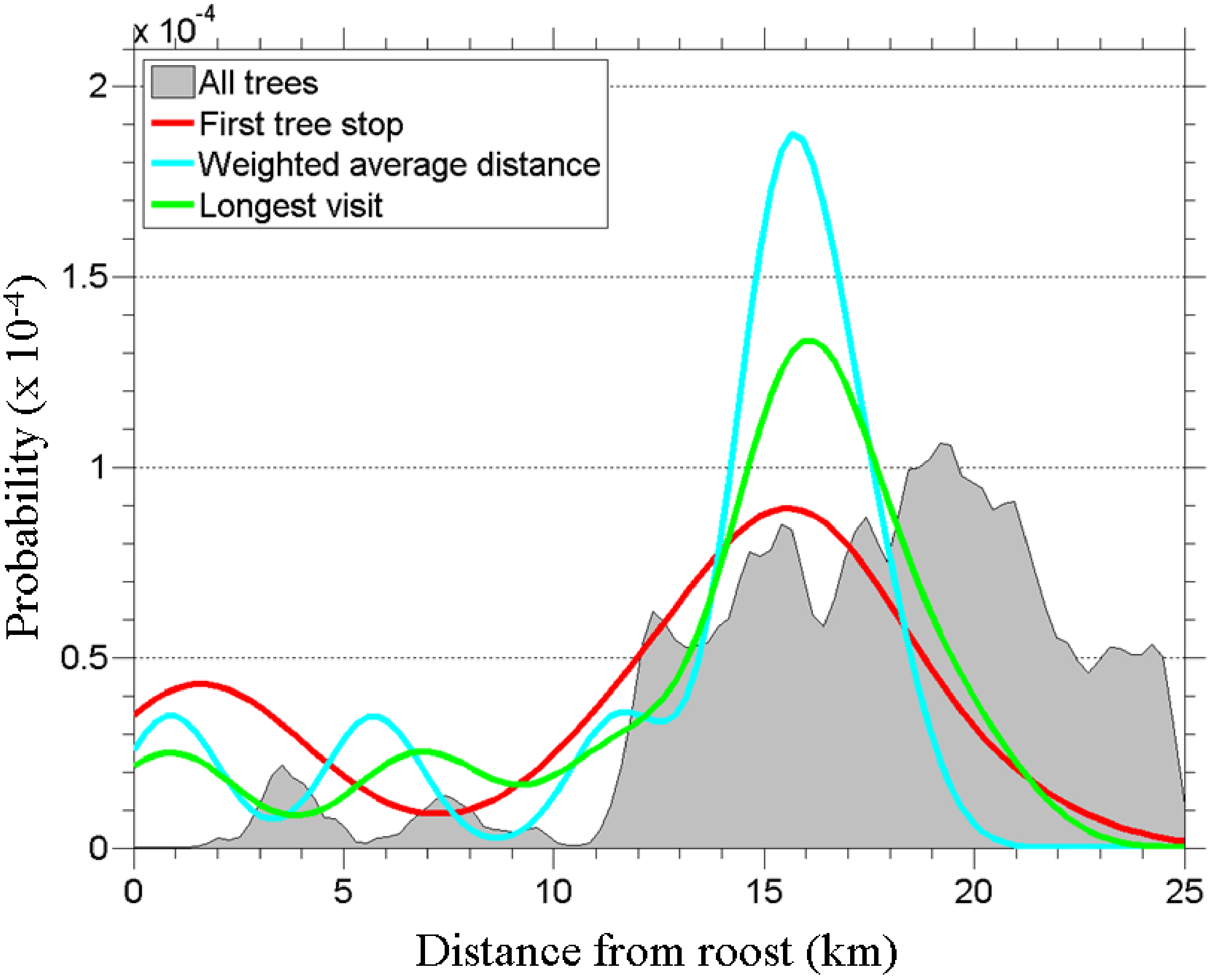


Figure 7: The locations selected by the bats (yellow dots) plotted on the attractiveness map. The three columns represent the whole non-commuting foraging track (quiescent and local flight, left), all stops (quiescent, middle) and the stops only in fruit trees (right). The two rows represent the ten bats with full night tracking (top), or the twenty two bats for which foraging data by GPS tracking is available (bottom). The green triangle represents the main roost.

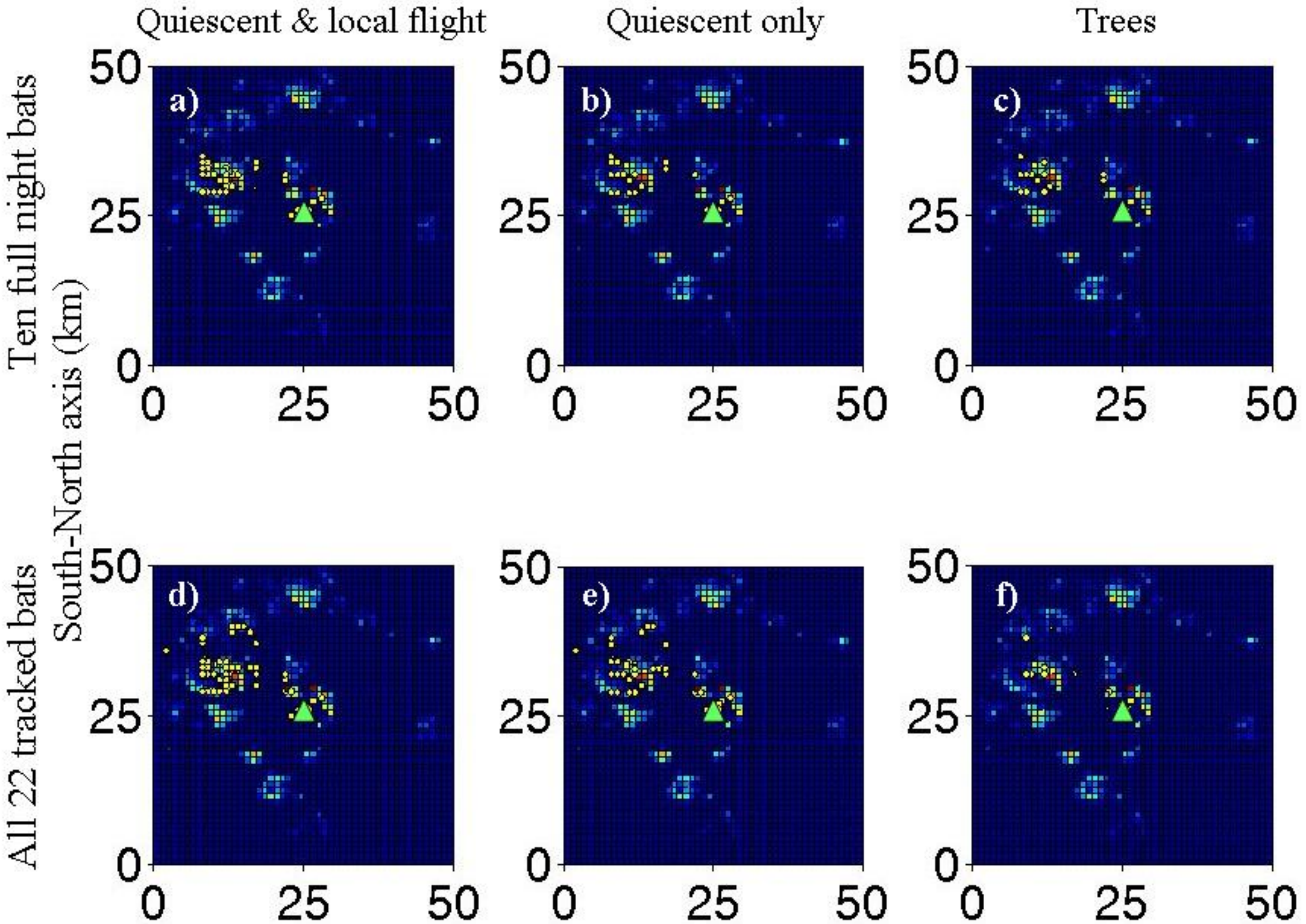


Figure 8: Histograms of attractiveness scores for different datasets of bat locations (red bars), contrasted against the histogram of all cells of the attractiveness map that are within 25 km from the roost and have non-zero attractiveness score (gray bars). For the upper two rows, the three columns represent the whole non-commuting foraging track (quiescent and local flight, left), all stops (quiescent, middle) and the stops only in fruit trees (right). The two upper rows represent the ten bats with full night tracking (top), or the twenty two bats for which foraging data by GPS tracking is available (middle). Panel (g) shows the histogram of the attractiveness score of the nearest fruit trees along the flight tracks of the 22 bats, only one of them visited by the bat. Note that nearly all nearest trees ignored by the bats have low attractiveness score.

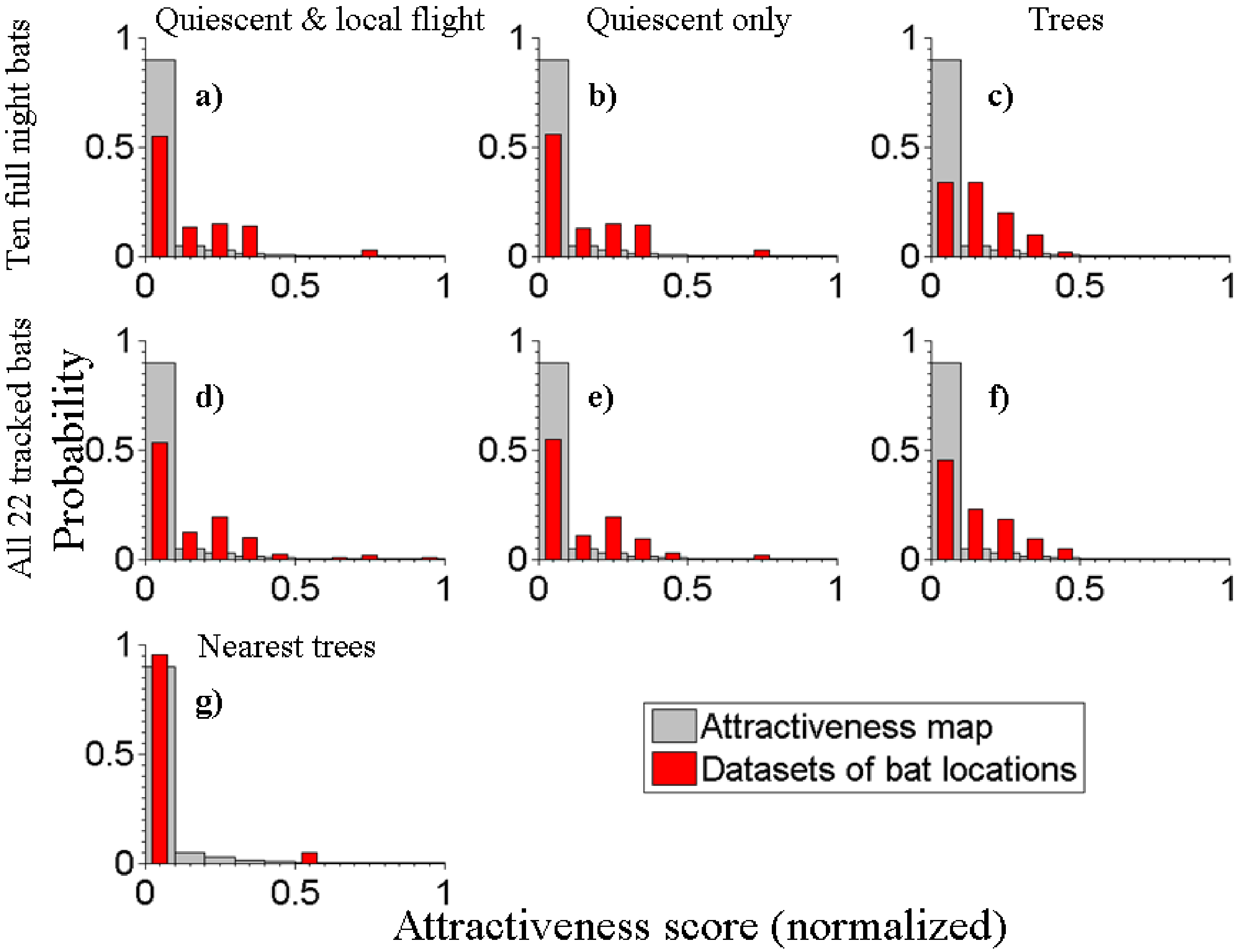


Figure 9: The mean attractiveness score of sites (1km^2 grid cell) visited by bats (black arrow) compared to the distribution of the mean attractiveness score in simulations of randomly foraging virtual bats, repeated 15,000 times for each dataset (blue). The three columns represent the whole non-commuting foraging track (quiescent and local flight, left), all stops (quiescent, middle) and the stops only in fruit trees (right). The two rows represent the ten bats with full night tracking (top), or the twenty two bats for which foraging data by GPS tracking is available (bottom). The red arrow represents the attractiveness score of the 22 nearest tree of the same species and ripeness as that selected by the bats. Note that these nearest fruit trees have a relatively low mean attractiveness score.

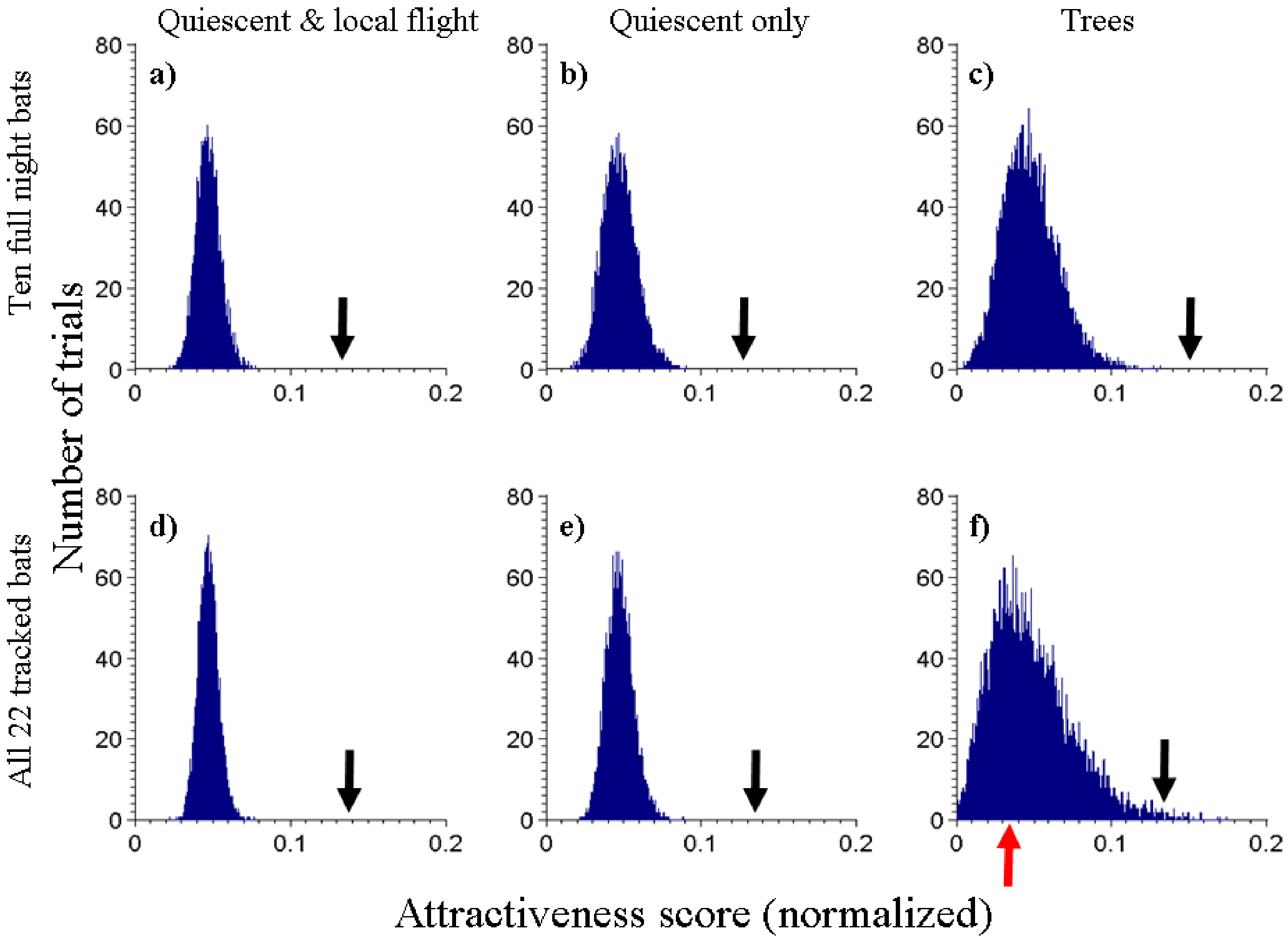
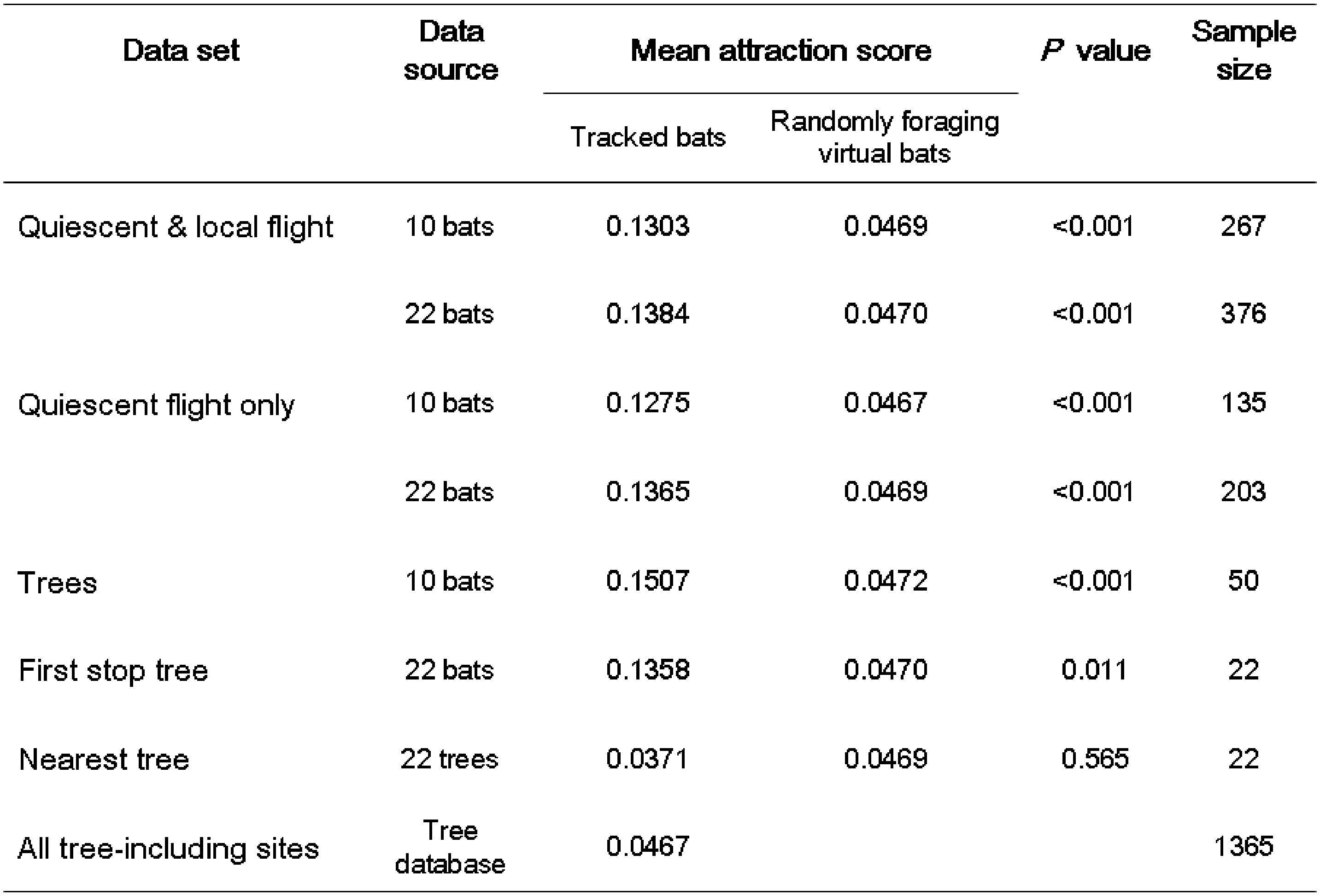


Table 3: Mean attractiveness score of sites (1km^2 grid cell) visited by bats compared to randomly selected sites that correspond to seven different datasets, assessed by Monte Carlo simulations. The three basic datasets were (a) quiescent locations (where bats were resting or sauntering) and local flights (20 s track with ground speed > 2.78 m/s and at a cumulative distance of less than 5 km), (b) only quiescent locations, and (c) the locations of all fruit trees selected by the bats. Three datasets were created for 10 full night tracks and three other datasets were created for all 22 foraging bats. A seventh reference dataset included the 22 nearest trees to the roost of the same species and ripeness as the fruit trees selected by the bats. For each dataset, the mean attractiveness score of the real foraging track of all bats is calculated, and compared to the mean attractiveness scores of the same number of virtual bats moving in the landscape in a random manner. The number of cells for each dataset is reported in the Sample size column. Simulations of randomly foraging virtual bats were repeated 15,000 times for each dataset to calculate the probability, reported in the *P* value column, of obtaining a mean attractiveness score equal or greater than the observed score. The bottom row provides the mean attractiveness score of all 1365 sites within a radius of 25 km from roost that include at least one fruit tree.



Data set	**Data source**	**Mean attraction score**		***P* value**	**Sample size**
		Tracked bats	Randomly foraging virtual bats		
Quiescent & local flight	10 bats	0.1303	0.0469	<0.001	267
	22 bats	0.1384	0.0470	<0.001	376
Quiescent flight only	10 bats	0.1275	0.0467	<0.001	135
	22 bats	0.1365	0.0469	<0.001	203
Trees	10 bats	0.1507	0.0472	<0.001	50
First stop tree	22 bats	0.1358	0.0470	0.011	22
Nearest tree	22 trees	0.0371	0.0469	0.565	22
All tree-including sites	Tree database	0.0467			1365

Table 4: Variety of fruit trees observed to be visited by the bats.

English name	Species name	Status of species in research area	Remarks
Apricot	***Prunus armeniaca*** L.	Cultivate	
Black mulberry	***Morus alba*** L.	Garden / Invasive	
California Fan Palm	***Washingtonia filifera*** (Linden ex André) H.Wendl. ex de Bary / ***Washingtonia robusta*** H.Wendl.	Garden/ Invasive	Two common garden trees, hard to differentiate between the species.
Carob	***Ceratonia siliqua*** L.	Native/ Cultivate	Common also in gardens
Chinese Banyan	***Ficus microcarpa*** L.f.	Garden	
Common Almond	***Amygdalus communis*** L.	Native / Cultivate	Fruit bats were observed feeding from green unripe fruit
Common fig	***Ficus carica*** L.	Native / Cultivate	Common also in gardens
European pear	***Pyrus communis*** L.	Cultivate	
Grey Elm	***Ulmus canescens*** Melville	Garden / Invasive	Personal observations of fruit bats feeding on buds.
Japanese Persimmon	***Diospyros kaki*** Thunb.	Cultivate	
Loquat	***Eriobotrya japonica*** (Thunb.) Lindl	Cultivate / Garden	
Mediterranean Cypress	***Cupressus sempervirens*** L.	Garden / Invasive	A fruit bat was observed feeding from its fruit
Olive tree	***Olea europaea*** L.	Native / Cultivate / Garden	
Palm date	***Phoenix dactylifera*** L.	Cultivated	
Passion fruit	***Passiflora edulis*** Sims	Garden	
Peach	***Prunus persica*** (L.) Stokes	Cultivate	
Persian lilac	***Melia azedarach*** L.	Garden / Invasive	
Rusty fig	***Ficus rubiginosa*** Desf. ex Vent.	Garden	
Stiff Bottlebrush	***Callistemon rigidus*** R.Br.	Garden	
Sycamore fig	***Ficus sycomorus*** L.	Introduced / Garden	Common also in gardens. Cultivated in the past
Tangerine	***Citrus reticulata*** Blanco	Cultivate / garden	
White mulberry	***Morus alba*** L. var. alba	Garden / Invasive	

Discussion and conclusions

We found that Egyptian fruit bats act as central place foragers, showing a medium-high fidelity to their focal roost. This result is in agreement with previous qualitative knowledge on the species in Israel (Makin 1990). Yet, our estimated probability of 0.58 for a tagged bat to occur in the focal roost during a random visit is relatively low compared with other obligatory cave-dwelling bats elsewhere in the world (Lewis 1995; Kunz & Lumsden 2003). This might be attributed to the relatively short duration of our monitoring scheme (35 days), and the fact that five bats that were lost just after release were included in this analysis. It might also reflect roost avoidance due to capture trauma (Kunz, Hodgkison, & Weise 2009). Individual bats showed high fidelity to specific fruit trees. In fact, direct field observations by A.T. found some of the individual bats on the same tree branch night after night. High tree fidelity of fruit bats was also found by Makin (1990) and in other parts of the world (see the review by Marshall (1983)).

The median altitude above ground level and mean straightness index of the commuting flight trajectories suggest that bats do not search for new food items during the commuting phase (Benhamou 2007; Miller, Christman, & Estevez 2011) in accordance with previous findings on other fruit bats (Fleming *et al.* 1977; Heithaus *et al.* 1978; Morrison 1978a; Fleming & Heithaus 1986; Richter & Cumming 2005; Andrianaivoarivelo *et al.* 2011). The high altitude flight of the bats during their commuting flight can be explained as either an anti-predator avoidance strategy (Fenton *et al.* 1994a; Baxter *et al.* 2006) flying above the typical altitude of owls, although such an avoidance mechanism has not yet been rigorously tested. Alternatively, high altitude flights might reflect a navigational requirement for visual orientation (Tsoar *et al.* 2011a). Insectivorous bats are known to forage for insects at high altitudes (Fenton & Griffin 1997; McCracken *et al.* 2008), and recently, there is evidence that fruit bats also fly at high altitudes (Parsons *et al.* 2008) but the reason is yet unclear. Because this is the first time fruit bats have been tracked by GPS, we do not know the extent to which high altitude flights are common among fruit bats.

Bats flew at lower flight speeds than were predicted by the energetic flight model (Pennycuick 2008). The bat median foraging and commuting speed was 6.86 m/s and 9.28 m/s, respectively, while the model predicted foraging and commuting speeds of 9.2 m/s and 15.8 m/s, respectively. Our empirical results of the bats flight speed (table 1) have a relatively low variance and seem to correctly sample the flight speeds of the bats. Our results do not agree with the predicted flight speeds of both models. We found our bats fly at V_{mp} instead of V_{mr} as predicted by the Pennycuick model. While the Norberg & Rayner (1987) model predicts much slower flight speeds, this coincide to the results Grodzinski *et al.* (2009) found in their research on the flight speed of *Pipistrellus kuhlii*. Carpenter (1986) estimates V_{mp} for Rousettus by wind tunnel experiments to be around 5 m/s. This result may well indicate that other factors influence the bats' flight speed behavior due to social interaction or predation risk (Holderied & Jones 2009; Grodzinski *et al.* 2009).

When examining the distribution of foraging bats in relation to the distribution of its resources within the landscape, we found the foraging bats to show a similar spatial distribution relative to distance from the roost as the distribution of the resource. This pattern suggests that bats forage according to the ideal free distribution theory. This conclusion was strengthened by the fact that the mean angle from the roost to the foraging site is as would be expected by a random selection of trees within the landscape. Interestingly, when examining the mean distance of all foraging sites to the roost, we find the bats forage significantly closer to the roost than would be expected by chance (table 2). This result is strengthened by the fact that bats foraged within the 10% of the tree distribution closest to the roost.

We assume that tree density is an approximation to patch richness and that bats will prefer to forage at higher tree densities (Morrison 1978a; Fleming & Heithaus 1986; Cosson *et al.* 1999; McConkey & Drake 2007). On the other hand, distance from roost has been a good predictor of bat densities (Heithaus *et al.* 1978; Mcdonald-Madden *et al.* 2005; Rainho & Palmeirim 2011; Nakamoto *et al.* 2011) as predicted by the CPF theory (Olsson *et al.* 2008). Because of our nearly complete knowledge of the fruit tree location within the landscape, we were able to create an attractiveness model of the landscape. The attractiveness score was defined as the tree density (gain) within the cell divided by the cell's distance to the roost (cost of locomotion and predation risk). When examining the cells selected by the bats, we see that bats clearly select cells with high attractiveness scores. The mean attractiveness score was significantly different than would have been expected by a random selection. We found the bats' foraging movement to be affected by fruit tree density relative to their distance from the roost. We used the attractiveness map to examine if selecting the closest fruit trees is an optimal solution for the bats. The mean attractiveness score for the 'nearest trees' was significantly lower than that of the trees the bats actually selected. In the specific case we present here, the bats foraging farther away from the roost are showing an optimal foraging behavior, greater than if they would have been foraging on the same fruit tree species with similar ripeness but as close to the roost as possible.

Examining the bats behavior in accordance to Fleming's 'three decisions a fruit bat must make' (Fleming 1988) shows the bats fly straight, high and fast commuting flights for an average distance of 11 km. During their commuting flight, bats do not seem to be alert for food and move along regular flight paths. A similar foraging pattern was found by Morrison (1978), while tracking the Jamaican fruit bat (*Artibeus jamaicensis*) in Panama and by Heithaus & Fleming (1978) while tracking the short-tailed fruit bat (*Carollia perspicillata*). Morrison was puzzled by his findings (1978), and wrote, '*Radio-tagged bats flew night after night to distant fig trees, apparently ignorant of other suitably ripe fig trees several times closer to their daytime refuge. The fact that the bats commuted to the same distant tree for several successive nights of feeding made it even more perplexing as to why more importance was not given to minimizing this commuting distance*'. In attempt to explain his observations, Morrison (1978) created a model for optimal foraging movement for a refuging predator. In his model, he assumed a trade-off between search time and commuting time. He predicted that the additional time needed to commute to a more distant prey patch is balanced by the reduction in search time that would have been needed to find a closer patch. His simulations were later critically criticized by Bovet and Benhamou (1991), claiming that the measured overlap was only for consecutive steps and not calculated for the entire flight path. Regrettably, this work was discontinued. Morrison's model uses oversimplified assumptions that make it unrealistic (for example, a predator with very limited movement, and overlap only between consecutive moves and not by tracks). We assume bats have good knowledge of the landscape because of their longevity, high maneuverability and because their food is relatively predictable in space and time. We show in this research an alternative and simpler explanation regarding the attractiveness of patches within the landscape.

Tracking of foraging animals has been revolutionized by the technological advancement of the miniaturized GPS, and by the improvement of digitized GIS data (Nathan *et al*. 2008; Bridge *et al*. 2011). The present research has benefited from these two improvements, Cutting-edge GPS technology enabled tracking the movement of a relatively small animal with unprecedented accuracy, detail and duration. Where GIS tools enabled high resolution mapping of the food resources over the entire area. Such detailed information on movements and food resources has recently enabled new insights into foraging of free-ranging wild animals (Matthiopoulos 2003; Richter & Cumming 2005; Wakefield, Phillips, & Matthiopoulos 2009; Owen-Smith, Fryxell, & Merrill 2010; Rainho & Palmeirim 2011).

In future work, the quantification of food resources might be further improved by conducting an even more comprehensive survey of species diversity and seasonality of fruit trees. Yet, the main additional information we need is on bat density across the landscape, and the movements of bats from other roosts. Furthermore, in the present research, we assumed a simple linear relationship between site attractiveness and tree density and a simple hyperbolic relationship (1/x) with the distance from the roost. Other, mechanistically derived, relationships are desired, as well as a sensitivity analysis to examine the robustness of our results with respect to alternative functional forms of these relationships

As already noted, the study of animal movement is being revolutionized by new technology and theory; yet, our ability to analyze and model such data has lagged behind (Jonsen *et al.* 2003). There is a growing need for new analytical as well as conceptual tools for analyzing such data. Although GPS devices can be very accurate, it was still impossible to differentiate between a resting bat on a tree and bats feeding and moving small distances within a tree. Acceleration measurements could differentiate between such behavior (Holland *et al.* 2009). Applying GPS plus acceleration device to Egyptian fruit bats was technically not possible for this study due to limitation on the mass of the tracking device, yet sufficiently light devices are currently under development. Other desired improvements in power supply would enable longer tracking durations in order to get more rigorously examining how the animals switch between foraging sites. Finally the continuing reduction in the cost of tracking equipment, will make ti possible to attach a larger number of devices and answer questions regarding the social interactions between members of the same colony, as well as between colonies.

Two interesting questions that we have as yet been unable to answer are: ’How do the bats select a foraging site?’ And: ‘To what extent do social interactions affect the bats’ site selection?’ These questions can be partially answered by sampling the most attractive areas (as predicted by the attractiveness map created in the present research) and monitoring bat behavior within these sites.

One of the major methodological limitations in the present research was the need to retrieve the GPS tag in order to download the data collected within it. This drastically limited our sample size and our ability to monitor the foraging bats in real time in the field. We hope that, in the near future, it will be possible to work with GPS devices that can transmit the location data in real time as well as to recharge the battery by remote control. By enabling these two possibilities, we will be able to monitor the reaction of bats to different stimuli in the field. For example, by creating an artificial tree and examining which, when, and how do the bats reach the new fruit tree, and how did they change their flight path and parameters to reach the target.

References

Abdi, H. (2007) The Bonferonni and Šidák Corrections for Multiple Comparisons. In: Salkind, N., (ed.). *Encyclopedia of Measurement and Statistics.* Sage Publication, Thousand Oaks.

Abramsky, Z., Rosenzweig, M.L., Pinshow, B., Brown, J.S., Kotler, B. & Mitchell, W.A. (1990) Habitat Selection - an Experimental Field-Test With 2 Gerbil Species. *Ecology*, **71**, 2358-2369.

Aldridge, H.D.J.N. & Brigham, R.M. (1988) Load Carrying and Maneuverability in an Insectivorous Bat: a Test of the 5 % “Rule” of Radio- Telemetry. *Journal of Mammalogy*, **69**, 379-382.

Andrianaivoarivelo, A.R., Ramilijaona, O.R., Racey, P. A., Razafindrakoto, N. & Jenkins, R.K.B. (2011) Feeding ecology, habitat use and reproduction of *Rousettus madagascariensis* Grandidier, 1928 (Chiroptera: Pteropodidae) in eastern Madagascar. *Mammalia*, **75**, 69-78.

Andrianaivoarivelo, A.R., Shore, G.D., McGuire, S.M., Jenkins, R.K.B., Ramilijaona, O., Louis, E.E. & Brenneman, R. A. (2008) Characterization of 22 microsatellite marker loci in the Madagascar rousette (*Rousettus madagascariensis*). *Conservation Genetics*, **10**, 1025-1028.

Barclay, R.M.R. & Jacobs, D.S. (2011) Differences in the foraging behaviour of male and female Egyptian fruit bats (*Rousettus aegyptiacus*). *Canadian Journal of Zoology*, **89**, 466-473.

Baxter, D.J.M., Psyllakis, J.M., Gillingham, M.P. & O’Brien, E.L. (2006) Behavioural Response of Bats to Perceived Predation Risk while Foraging. *Ethology*, **112**, 977-983.

Benhamou, S. (2007) How many animals really do the Levy walk? *Ecology*, **88**, 1962-1969.

Bovet, P. & Benhamou, S. (1991) Optimal Sinuosity in Central Place Foraging Movements. *Animal Behaviour*, **42**, 57-62.

Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Kays, R., Kelly, J.F., Robinson, W.D. & Wikelski, M. (2011) Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. *BioScience*, **61**, 689-698.

Carpenter, R.E. (1986) Flight physiology of intermediate-sized fruit bats (Pteropodidae). *Journal of Experimental Biology,***120**, 79-103.

Chapman, C.A., Wrangham, R.W., Chapman, L.J., Kennard, D.K. & Zanne, A.E. (1999) Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*, **15**, 189-211.

Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, **9**, 129-136.

Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., LaFrankie, J.V., Lee, H.S., Losos, E., Manokaran, N., Sukumar, R. & Yamakura, T. (2000) Spatial patterns in the distribution of tropical tree species. *Science*, **288**, 1414-1418.

Cosson, J.-françois, Pons, J.-marc & Masson, D. (1999) Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *Journal of Tropical Ecology*, **15**, 515-534.

Eby, P. (1991) Seasonal Movements of Gray-Headed Flying-Foxes, *Pteropus poliocephalus* (Chiroptera, Pteropodidae), from 2 Maternity Camps in Northern New-South-Wales. *Wildlife Research*, **18**, 547-559.

Fenton, M.B. & Griffin, D.R. (1997) High-Altitude Pursuit of Insects by Echolocating Bats. *Journal of Mammalogy*, **78**, 247-250.

Fenton, M.B., Rautenbach, I.L., Smith, S.E., Swanepoel, C.M., Grosell, J. & Van Jaarsveld, J. (1994) Raptors and bats: threats and opportunities. *Animal Behaviour*, **48**, 9-18.

Fleming. (1988) *The Short-tailed Fruit Bat: A Study in Plant-Animal Interactions*. University of Chicago Press, Chicago.

Fleming, T.H. & Heithaus, E.R. (1986) Seasonal Foraging Behavior of the Frugivorous Bat Carollia-Perspicillata. *Journal of Mammalogy*, **67**, 660-671.

Fleming, T.H., Heithaus, E.R. & Sawyer, W.B. (1977) Experimental-Analysis of Food Location Behavior of Frugivorous Bats. *Ecology*, **58**, 619-627.

Fretwell, S.D. (1972) Populations in a seasonal environment. *Monographs in Population Biology*, **5**, 1-217

Fretwell, S.D. & Lucas Jr., H.L. (1969) On territorial behavioral and other factors influencing habitat distribution in birds: I. Theoretical development. *Acta Biotheoretica*, **19**, 16-36.

Grodzinski, U., Spiegel, O., Korine, C. & Holderied, M.W. (2009) Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*. *Journal of Animal Ecology*, **78**, 540-8.

Hamilton, W.J., Gilbert, W.M., Heppner, F.H. & Planck, R.J. (1967) Starling Roost Dispersal and a Hypothetical Mechanism Regulating Rhythmical Animal Movement to and from Dispersal Centers. *Ecology*, **48**, 825-&

Hamilton, W.J.& Watt, K.E.F. (1970) Refuging. *Annual Review of Ecology and Systematics*, **1**, 263-286.

Hampe, A. (2003) Large-scale geographical trends in fruit traits of vertebrate-dispersed temperate plants. *Journal of Biogeography*, **30**, 487-496.

Hebblewhite, M. & Haydon, D.T. (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2303-2312.

Heithaus, E.R., Fleming, T.H. (1978) Foraging Movements of a Frugivorous Bat, *Carollia perspicillata* (Phyllostomatidae). *Ecological Monographs*, **48**, 127-143.

Holderied, M.W. & Jones, G. (2009) Flight dynamics of bats. *Ecological and behavioral methods for the study of bats*, 2nd ed (eds T.H. Kunz & S. Parsons). The John Hopkins University Press, Baltimore.

Holland, R.A., Wikelski, M., Franz, K. & Bosque, C. (2009) The Secret Life of Oilbirds: New Insights into the Movement Ecology of a Unique Avian Frugivore. *PloS ONE*, **4**, 1-6.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Inchausti, P., Hector, A., Lavorel, S., Lawton, J.H., Lodge, D., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. *Ecological Monographs*, **75**, 3-36.

Izhaki, I., Korine, C. & Arad, Z. (1995) The effect of bat (*Rousettus aegyptiacus*) dispersal on seed-germination in eastern Mediterranean habitats. *Oecologia*, **101**, 335-342.

Jacobsen, N.H.G. & Du Plessis, E. (1976) Observations on the ecology and biology of the Cape Fruit bat *Rousettus aegyptiacus leachi* in the eastern Transvaal. *South African Journal of Science*, **72**, 270-273.

Jacobsen, N.H.G., Viljoen, P.C. & Ferguson, W. (1986) Radio tracking of problem fruit bats (*Rousettus aegyptiacus*) in the Transvaal with notes on flight and energetics. *Zeitschrift fur Saugetierkunde-International Journal of Mammalian Biology*, **51**, 205-208.

Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, **8**, 93-115.

Jonsen, I.D., Myers, R.A. & Flemming, J.M. (2003) Meta-analysis of animal movement using state-space models. *Ecology*, **84**, 3055-3063.

Kalko, E.K.V., Herre, E.A. & Handley, C.O. (1996) Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *Journal of Biogeography*, **23**, 565-576.

Kaplan, E.D. & Hegarty, C. (2005) *Understanding GPS: Principles and Applications,* 2nd ed. Artech House Publishers, Norwood.

Kennedy, M. & Gray, R.D. (1993) Can Ecological Theory Predict the Distribution of Foraging Animals - a Critical Analysis of Experiments On the Ideal Free Distribution. *Oikos*, **68**, 158-166.

Korine, C., Izhaki, I. & Arad, Z. (1998) Comparison of fruit syndromes between the Egyptian fruit-bat (*Rousettus aegyptiacus*) and birds in East Mediterranean habitats. *Acta Oecologica*, **19**, 147-153.

Korine, C., Izhaki, I. & Arad, Z. (1999) Is the Egyptian fruit-bat *Rousettus aegyptiacus* a pest in Israel? An analysis of the bat's diet and implications for its conservation. *Biological Conservation*, **88**, 301-306.

Korine, C., Izhaki, I. & Makin, D. (1994) Population-structure and emergence order in the Fruit-bat (*Rousettus aegyptiacus*, MAMMALIA, CHIROPTERA). *Journal of Zoology*, **232**, 163-174.

Krivan, V., Cressman, R. & Schneider, C. (2008) The ideal free distribution: A review and synthesis of the game-theoretic perspective. *Theoretical Population Biology*, **73**, 403-425.

Kunz, T.H. & Lumsden, L.F. (2003) Ecology of cavity and foliage roosting bats. *Bat Ecology* (eds T.H. Kunz & M.B. Fenton), pp. 3-89. The University of Chicago Press, Chicago.

Kunz, T.H., Hodgkison, R. & Weise, C.D. (2009) Methods for capturing and handling bats. *Ecological and behavioral methods for the study of bats*, 2nd ed (eds T.H. Kunz & S. Parsons), pp. 3-35. The John Hopkins University Press, Baltimore.

Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, **1223**, 1-38.

Kwiecinski, G.G. & Griffiths, T.A. (1999) *Rousettus egyptiacus*. *Mammalian Species*, **611**, 1-9.

Lewis, S.E. (1995) Roost fidelity of bats - a review. *Journal of Mammalogy*, **76**, 481-496.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of patchy environment. *American Naturalist*, **100**, 603-609.

Makin, D. (1990) *Aspects of the Biology of the Fruit Bat Rousettus aegyptiacus in Israel*. Tel-Aviv University. PhD Thesis. In Hebrew.

Marshall, A.G. (1983) Bats , flowers and fruit: evolutionary relationships in the Old World. *Biological Journal of the Linnean Society*, **20**, 115-135.

Matthiopoulos, J. (2003) The use of space by animals as a function of accessibility and preference. *Ecological Modelling*, **159**, 239-268.

McCracken, G.F., Gillam, E.H., Westbrook, J.K., Lee, Y.-F., Jensen, M.L. & Balsley, B.B. (2008) Brazilian free-tailed bats (*Tadarida brasiliensis*: Molossidae, Chiroptera) at high altitude: links to migratory insect populations. *Integrative and Comparative Biology*, **48**, 107-18.

McConkey, K.R. & Drake, D.R. (2007) Indirect Evidence that Flying Foxes Track Food Resources Among Islands in a Pacific Archipelago. *Biotropica*, **39**, 436-440.

Mcdonald-Madden, E., Schreiber, E.S.G., Forsyth, D.M., Choquenot, D. & Clancy, T.F. (2005) Factors affecting Grey-headed Flying-fox (*Pteropus poliocephalus*: Pteropodidae) foraging in the Melbourne metropolitan area, Australia. *Austral Ecology*, **30**, 600-608.

Miller, C., Christman, M.C. & Estevez, I. (2011) Movement in a confined space Estimating path tortuosity. *Applied Animal Behaviour Science*, **135**, 13-23.

Mills, K.J., Patterson, B.R. & Murray, D.L. (2006) Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. *Wildlife Society Bulletin*, **34**, 1463-1469.

Morrison, D.W. (1978) Optimal searching strategy for refuging predators. *American Naturalist*, **112**, 925-934.

Muscarella, R. & Fleming, T.H. (2007) The role of frugivorous bats in tropical forest succession. *Biological Reviews*, **82**, 573-590.

Nakamoto, A., Itabe, S., Sato, A., Kinjo, K. & Izawa, M. (2011) Geographical distribution pattern and interisland movements of Orii's flying fox in Okinawa Islands, the Ryukyu Archipelago, Japan. *Population Ecology*, **53**, 241-252.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19052-19059.

Norberg, U.M. & Rayner, J.M.V. (1987) Echological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **316**, 335-427.

Olsson, O., Brown, J.S. & Helf, K.L. (2008) A guide to central place effects in foraging. *Theoretical population biology*, **74**, 22-33.

Orians, G.H. & Pearson, N.E. (1979) On the theory of central place foraging. *Analysis of Ecological Systems* (eds D.J. Horn, R.D. Mitchell & G.R. Stairs), pp. 154-177. Ohio State University Press, Ohio.

Owen-Smith, N., Fryxell, J.M. & Merrill, E.H. (2010) Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**, 2267-2278.

Parry-Jones, K.A. & Augee, M.L. (2001) Factors affecting the occupation of a colony site in Sydney, New South Wales by the Grey-headed Flying-fox *Pteropus poliocephalus* (Pteropodidae). *Austral Ecology*, **26**, 47-55.

Parsons, J.G., Blair, D., Luly, J. & Robson, S.K.A. (2008) Flying-fox (Megachiroptera: Pteropodidae) flight altitudes determined via an unusual sampling method: aircraft strikes in Australia. *Acta Chiropterologica*, **10**, 377-379.

Pennycuick, C.J. (1989) *Bird Flight Performance: A Practical Calculation Manual*. Oxford University Press, Oxford.

Pennycuick, C.J. (2008) *Modelling the Flying Bird*. Academic Press, London.

Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, **15**, 523-575.

Rainho, A. & Palmeirim, J.M. (2011) The importance of distance to resources in the spatial modelling of bat foraging habitat. *PloS ONE*, **6**, e19227.

Rayner, J.M.V. (1999) Estimating power curves of flying vertebrates. *Journal of Experimental Biology*, **202**, 3449-3461.

Richter, H.V. & Cumming, G.S. (2005) Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *Journal of Zoology*, **268**, 35-44.

Robinson, W.D., Bowlin, M.S., Bisson, I., Shamoun-Baranes, J., Thorup, K., Diehl, R.H., Kunz, T.H., Mabey, S. & Winkler, D.W. (2010) Integrating concepts and technologies to advance the study of bird migration. *Frontiers in Ecology and the Environment*, **8**, 354-361.

Rosenberg, D.K. & McKelvey, K.S. (1999) Estimation of habitat selection for central-place foraging animals. *The Journal of Wildlife Management*, **63**, 1028-1038.

Shanahan, M. & Compton, S.G. (2001) Vertical stratification of figs and fig-eaters in a Bornean lowland rain forest: how is the canopy different? *Plant Ecology*, **153**, 121-132.

Shilton, L.A., Altringham, J.D., Compton, S.G. & Whittaker, R.J. (1999) Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 219-223.

Sih, A., Petranka, J.W. & Kats, L.B. (1988) The Dynamics of prey refuge use – a model and test with sunfish and Salamander larvae. *The American Naturalist*, **132**, 463-483.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton.

Tang, Z., Chen, Z., Ma, J., Zhu, G., Ma, X., Sheng, L. & Li, Y. (2010) Foraging areas of *Rousettus leschenaulti* on the Hainan Island of China. *Current Zoology*, **56**, 479-484.

Tregenza, T. (1995) Building the ideal free distribution. *Advances in Ecological Research*, **26**, 253-307.

Tsoar, A., Nathan, R., Bartan, Y., Altstein, O., Vyssotski, A.L., Dell'Omo, G.D. & Ulanovsky, N. (2011a) Large scale map-like navigation memory in a mammal. *Proceedings of the National Academy of Sciences of the United States of America,***108,** E718-E724.

Tsoar, A., Shohami, D., Nathan, R., Years, F. & Ecology, I. (2011b) A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. *Fifty years of invasion ecology: the legacy of Carles Elton* (ed D.M. Richardson), pp. 101-120. Wiley-Blackwell, Oxford.

Vardon, M.J., Brocklehurst, P.S., Woinarski, J.C.Z., Cunningham, R.B., Donnelly, C.F. & Tidemann, C.R. (2001) Seasonal habitat use by flying-foxes, *Pteropus alecto* and *P. scapulatus* (Megachiroptera), in monsoonal Australia. *Journal of Zoology*, **253**, 523-535.

Wakefield, E., Phillips, R. & Matthiopoulos, J. (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series*, **391**, 165-182.

Welbergen, J. a. (2006) Timing of the evening emergence from day roosts of the grey-headed flying fox, *Pteropus poliocephalus*: the effects of predation risk, foraging needs, and social context. *Behavioral Ecology and Sociobiology*, **60**, 311-322.

Winter, Y. (1999) Flight speed and body mass of nectar-feeding bats (Glossophaginae) during foraging. *Journal of Experimental Biology*, **202**, 1917–1930.

CHAPTER 2

Large-scale navigational map in a mammal

Article:

Tsoar, A., Nathan, R. Bartan, Y., Vyssotski, A.L., Dell'Omoc, G. and Ulanovsky, N. (2011) Large-scale navigational map in a mammal. *Proceedings of the National Academy of Science.* 108(37):E718-E724.

DOI: 10.1073/pnas.1107365108

Large-scale navigational map in a mammal

Asaf Tsoar[a,1,2], Ran Nathan[a,2,3], Yoav Bartan[a], Alexei Vyssotski[b], Giacomo Dell'Omo[c], and Nachum Ulanovsky[d,2,3]

[a]*Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, Hebrew University of Jerusalem, Jerusalem 91904, Israel;* [b]*Institute of Neuroinformatics, University of Zurich/Swiss Federal Institute of Technology (Eidgenössische Technische Hochschule) Zurich, Zurich CH-8057, Switzerland;* [c]*Ornis italica, 00199 Rome, Italy; and* [d]*Department of Neurobiology, Weizmann Institute of Science, Rehovot 76100, Israel*

AUTHOR SUMMARY

Navigation is critical for the survival of animals and has been extensively studied, mostly in nonmammalian species (1–4). The most advanced type of navigation is the ability to travel directly to a certain destination from any starting point in the environment, regardless of its direction and without relying on familiar routes. Evidence for the existence of such navigational map comes from field and laboratory experiments. In the field, homing experiments in translocated lobsters (3) and pigeons (1, 4), for example, showed an ability to navigate from an unfamiliar site to one or more goal locations. Typically, inferences from such homing experiments were based either on animals' vanishing bearing at the release site—that is, the direction in which the animal vanished after release—or based on animals' reappearance at the goal location. Only recently were translocated pigeons and honeybees tracked continuously (2, 4); yet, to date, no high-resolution movement tracks have been collected from free-ranging mammals homing from translocation distances larger than a few kilometers—and the lack of such data severely limits our understanding of mammalian navigation mechanisms. In the laboratory, various experimental approaches have suggested the existence of a mental representation of space, or a "cognitive map" in rodents (5); yet, the inference of map-like navigation from laboratory experiments on such small spatial scale (i.e., meters) has been questioned. Thus, there is a gap in knowledge about mammalian navigation: most of our knowledge about large-scale navigation comes from studies in nonmammalian species, whereas detailed data on mammals' navigation in the field is scarce, certainly compared with data obtained from birds.

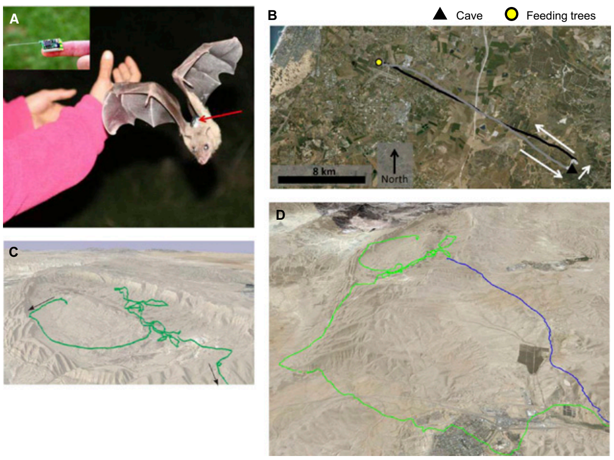


Fig. P1. (*A*) GPS device placed on the back of an Egyptian fruit bats. Photo credit: A. Tsoar. (*B*) Flight trajectory of a bat leaving the cave, flying locally (light gray line), then taking a long commuting flight to the feeding tree (black line) and then back to the cave (dark gray). Bats flew at very straight trajectories, and returned to the same favorite feeding-trees night after night. (*C*) Bat that was released in the Negev desert in Israel, inside a deep erosional crater that is surrounded by cliffs approximately 300-m high. Note the tortuous disoriented flight (green): this bat flew almost 34 km before it eventually left the crater and turned toward the familiar area. (*D*) Bats that were released from a high mountain at the crater edge have homed straight (blue line), in contrast to the disoriented flights of bats released inside the crater (green), suggesting an important role for vision in Egyptian fruit bat navigation. *C*, view from northeast; *D*, view from north-northeast.

Here, we have set out to close this gap by examining whether a free-ranging mammal performs map-like navigation on large scales (~100 km). To this end, we developed a highly miniaturized global positioning system (GPS) datalogger device (Fig. P1*A*). We equipped cave-dwelling Egyptian fruit bats (*Rousettus aegyptiacus*) with these devices, which enabled high-resolution measurements of the bats' flight trajectories over several consecutive nights. We asked whether bats possess a cognitive map of their visually familiar environment, which would be manifested by their ability to perform novel short-cuts within this environment, and whether they are capable of homing back to their cave when translocated outside their visually familiar environment.

When bats were released at their cave, they undertook high, fast, and very straight commuting flights from their cave to remote fruit trees (Fig. P1*B*). Bats returned to the same individual trees night after night, from distances of tens of kilometers, demonstrating superb navigational abilities. When translocated 44 km south of their cave, bats homed directly to one of two goal locations—familiar fruit tree or cave—ruling out beaconing, route-following, or path-integration mechanisms. Bats released 84 km south of their cave, within a deep natural crater, were initially disoriented (Fig. P1 *C* and *D*, green line), but eventually left the crater and flew in the direction of their home; in contrast, bats released at the crater-edge top homed directly (Fig. P1*D*, blue line). Although it is possible that celestial, magnetic, or olfactory cues contribute to long-range navigation in bats, the most parsimonious explanation for the dramatic behavioral differences between release at the crater edge (i.e., straight homing) and release inside the crater (i.e., disorientation) is visual, reflecting the availability of distal visual landmarks at the crater edge and the lack of familiar distal visual landmarks deep inside the crater. Thus, these data in Egyptian fruit bats suggest that navigation is primarily guided by self-triangulation based on distal visual landmarks.

Taken together, experimental releases at the roost as well as translocation studies suggest that (*i*) bats are capable of visual-based navigation within a familiar environment and

---

Author contributions: A.T., R.N., and N.U. designed research; A.T., Y.B., and N.U. performed research; A.V. and G.D. contributed new reagents/analytic tools; A.T., R.N., A.V., G.D., and N.U. analyzed data; and A.T., R.N., and N.U. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1] Present address: Israel Nature and Parks Authority, Beer Sheva 84215, Israel.

[2] To whom correspondence may be addressed: E-mail: asaf.tsoar@mail.huji.ac.il, rnathan@cc.huji.ac.il, or nachum.ulanovsky@weizmann.ac.il.

[3] R.N. and N.U. contributed equally to this work.

See full research article on page E718 of www.pnas.org.

Cite this Author Summary as: PNAS 10.1073/pnas.1107365108.

(*ii*) bats can home from outside their visually familiar environment. Further, these data provide evidence for two kinds of navigational capacities in bats. The first is a cognitive map of their visually familiar environment, similar to the map-based mechanism proposed previously for rodent navigation in a water maze (1) but studied here in a free-ranging mammal at five orders of magnitude larger spatial scale. Second, these data demonstrate the ability of bats to home from outside their visually familiar environment. Our findings provide unique evidence for either of these navigational capacities in bats, as well as evidence for large-scale navigation in a free-ranging wild mammal.

1. Gallistel CR (1990) *The Organization of Learning* (MIT Press, Cambridge, MA).
2. Menzel R, et al. (2005) Honey bees navigate according to a map-like spatial memory. *Proc Natl Acad Sci USA* 102:3040–3045.
3. Boles LC, Lohmann KJ (2003) True navigation and magnetic maps in spiny lobsters. *Nature* 421:60–63.
4. Lipp H-P, et al. (2004) Pigeon homing along highways and exits. *Curr Biol* 14: 1239–1249.
5. O'Keefe J, Nadel L (1978) *The Hippocampus as a Cognitive Map* (Oxford Univ Press, Oxford).

Large-scale navigational map in a mammal

Asaf Tsoar[a,1,2], Ran Nathan[a,2,3], Yoav Bartan[a], Alexei Vyssotski[b], Giacomo Dell'Omo[c], and Nachum Ulanovsky[d,2,3]

[a]Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, Hebrew University of Jerusalem, Jerusalem 91904, Israel; [b]Institute of Neuroinformatics, University of Zurich/Swiss Federal Institute of Technology (Eidgenössische Technische Hochschule) Zurich, Zurich CH-8057, Switzerland; [c]*Ornis italica*, 00199 Rome, Italy; and [d]Department of Neurobiology, Weizmann Institute of Science, Rehovot 76100, Israel

Edited by Charles R. Gallistel, Rutgers University, Piscataway, NJ, and approved July 13, 2011 (received for review May 8, 2011)

Navigation, the ability to reach desired goal locations, is critical for animals and humans. Animal navigation has been studied extensively in birds, insects, and some marine vertebrates and invertebrates, yet we are still far from elucidating the underlying mechanisms in other taxonomic groups, especially mammals. Here we report a systematic study of the mechanisms of long-range mammalian navigation. High-resolution global positioning system tracking of bats was conducted here, which revealed high, fast, and very straight commuting flights of Egyptian fruit bats (*Rousettus aegyptiacus*) from their cave to remote fruit trees. Bats returned to the same individual trees night after night. When displaced 44 km south, bats homed directly to one of two goal locations—familiar fruit tree or cave—ruling out beaconing, route-following, or path-integration mechanisms. Bats released 84 km south, within a deep natural crater, were initially disoriented (but eventually left the crater toward the home direction and homed successfully), whereas bats released at the crater-edge top homed directly, suggesting navigation guided primarily by distal visual landmarks. Taken together, these results provide evidence for a large-scale "cognitive map" that enables navigation of a mammal within its visually familiar area, and they also demonstrate the ability to home back when translocated outside the visually familiar area.

cognitive map | spatial memory | true navigation | movement ecology | global positioning system

Navigation is critical for the survival of animals, and has been extensively studied in animals, mostly in nonmammalian species (1–10). The most advanced type of navigation is the ability to travel directly to a certain destination from any starting point in the environment, regardless of its direction and without relying on familiar routes. Evidence for the existence of such navigational map (11, 12) comes from field and laboratory experiments. In the field, homing experiments in translocated lobsters (13), newts (14) and pigeons (1, 15, 16), for example, showed an ability to navigate from an unfamiliar site to one or more goal locations. Typically, inferences from such homing experiments were based either on animals' vanishing bearing at the release site, or animals' reappearance at the goal location. Only recently were translocated pigeons and honey bees tracked continuously (3, 17); yet, to date, no high-resolution movement tracks have been collected from free-ranging mammals homing from translocation distances larger than a few kilometers—and the lack of such data severely limits our understanding of mammalian navigation mechanisms. In the laboratory, studies implementing various experimental approaches suggested the existence of a mental representation of space, or a "cognitive map," in rodents (2, 18–20); yet, our ability to infer map-like navigation from laboratory experiments on such small spatial scale (in meters) has been questioned (21, 22). Thus, there is a gap in knowledge about mammalian navigation: most of our knowledge about large-scale navigation comes from studies in nonmammalian species, whereas detailed data on mammals' navigation in the field is scarce, certainly compared with data on birds.

Here, we have set out to close this gap, by examining whether a free-ranging mammal performs map-like navigation on large scales (~100 km). We equipped cave-dwelling Egyptian fruit bats (*Rousettus aegyptiacus*) with miniature global positioning system (GPS) dataloggers (Fig. S1), which enabled high-resolution measurements of their flight trajectories over several consecutive nights (*Methods*). We asked whether bats possess a cognitive map of their visually familiar environment (2), which would be manifested by the ability to perform novel short-cuts within this environment—and whether they are capable of homing back to their cave when translocated outside their visually familiar environment. Our results, combining releases at the roost as well as translocation experiments, suggest that bats are capable of visual-based navigation within the familiar environment, and that they can also home from outside their visually familiar environment. These data thus provide evidence for both kinds of navigational capacities in bats—and evidence for large-scale navigation in a mammal.

Results

When released near their cave, individual bats commuted to distant fruit trees (Fig. 1 *A* and *B*, Fig. S2, and Movie S1) in long, fast, high, and very straight flights ($N = 15$ bats; mean straightness index ± SD, 0.97 ± 0.02; Fig. 1 *B* and *D*, Table 1, and Fig. S3). Commuting flight speeds were typically between 35 and 55 km/h (Fig. 1*B*, *Top*), and flight heights were typically at a few hundred meters above ground level (Fig. 1*B*, *Bottom*). All but one bat flew straight to a feeding tree without following landscape elements. Bats typically did not fly to the fruit tree nearest to their cave; instead, they flew to remote fruit trees, passing many similar fruiting trees on the way (Fig. S4). When they had arrived at the favored tree, bats typically foraged at this tree and at adjacent trees for the entire night (Movie S1). Moreover, the bats returned to the same fruit tree over several consecutive nights (Fig. 1*E*, *Inset*, arrow), often following the same trajectory every night (Fig. 1*F*, "flyway"). Of the 15 bats for which we collected foraging data, 14 bats had GPS and/or radiotelemetry data from consecutive nights, and 13 of these 14 bats (93%) returned to the same tree in at least two nights within the first three nights from release. Moreover, radiotelemetry tracking of 16 additional fruit bats from the same colony showed that bats foraged on the same tree for as long as 4 mo.

The fast and very straight repetitive flights to the same fruit tree, night after night, might be explained by navigation toward a specific sensory cue ["beaconing" (2)], or navigation via a sequence of landmarks or along a learned vector. Olfactory bea-

---

Author contributions: A.T., R.N., and N.U. designed research; A.T., Y.B., and N.U. performed research; A.V. and G.D. contributed new reagents/analytic tools; A.T., R.N., A.V., G.D., and N.U. analyzed data; and A.T., R.N., and N.U. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]Present address: Israel Nature and Parks Authority, Beer Sheva 84215, Israel.

[2]To whom correspondence may be addressed: E-mail: asaf.tsoar@mail.huji.ac.il, rnathan@cc.huji.ac.il, or nachum.ulanovsky@weizmann.ac.il.

[3]R.N. and N.U. contributed equally to this work.

See Author Summary on page 15031.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1107365108/-/DCSupplemental.

www.pnas.org/cgi/doi/10.1073/pnas.1107365108

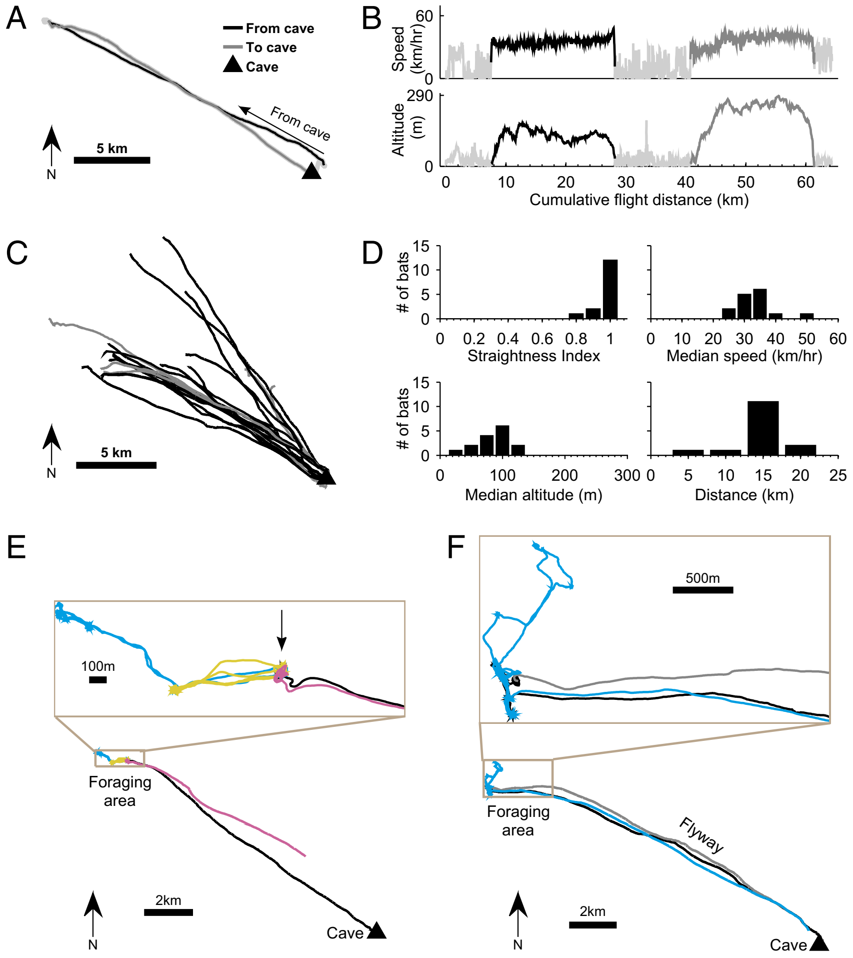


Fig. 1. GPS tracking of Egyptian fruit bats navigating from their cave. (*A*) Example of bat 125 leaving the cave, flying locally (light gray line), then taking a long commuting flight to the feeding tree (black line) and back to the cave (dark gray). (*B*) Speed and altitude above ground level for the same bat as in *A* as function of its cumulative flight distance during the night. Black, commuting flight from cave; dark gray, back to cave. (*C*) All commuting flights that started or ended directly at the cave ($n = 14$); colors as in *A*; note the very straight flights of all these bats. An additional seven flights were composed of a local flight and then a commuting flight (e.g., the bat in *A*); their commuting flights were as straight as those depicted here. (*D*) Flight parameters for the commuting flights of all bats released at the cave ($n = 15$): shown are straightness index, median speed, median altitude above ground level, and total flight distance to the first feeding tree. (*E* and *F*) Bats returned to the same individual tree night after night. *Bottom*: Full flight path; *Top* (*Inset*): Zoom-in view of the feeding trees; colors represent different consecutive nights. (*E*) Bat 213 returned over four consecutive nights to the same *Prunus armeniaca* tree (arrow). (*F*) Bat 243 returned over two nights to the same two trees; note the commuting flyway; black and gray lines represent flight to and from the foraging area on night one.

coning toward the tree itself is unlikely caused by the presence of numerous fruit trees of the same species and of similar fruit ripeness along the flyway and in the surroundings (Fig. S4). Visual beaconing to the tree is unlikely because most of the favored trees were not located near any light source to which the bat might beacon; similarly, when flying back to the cave, visual beaconing was unlikely because no light sources are found within 1 km from the cave. Nevertheless, the bats might have beaconed toward the odors of the sea, or toward a distant visual cue in line with the direction of the feeding tree. Such navigation, performed from different starting positions (eg, cave, trees), requires knowledge about the relative geometric locations of multiple goals of interest and multiple distant cues—consistent with map-based navigation (1, 2).

Table 1. Summary statistics of data from bats released at the cave and at the 3 translocation points (release sites R1, R2 and R3)

Characteristic	Cave	R1	R2 (crater in)	R3 (crater out)
No. of bats	15	10	7	4
Speed, km/h	33.5 ± 5.5 (26.8–49.3)	35.3 ± 8.2 (26.2–51.7)	31.3 ± 2.0 (27.6–34.3)	48.1 ± 2.2 (45.9–50.8)
Altitude above ground level, m	84.0 ± 27.4 (31.3–122.0)	55.1 ± 30.3 (13.7–102.2)	51.4 ± 12.9 (27.6–64.7)	76.1 ± 20.6 (59.1–103.1)
Flight distance, km	15.0 ± 3.2 (7.1–20.6)	42.7 ± 15.8 (10.4–62.2)	50.5 ± 32.4 (5.5–98.5)	51.8 ± 47.0 (5.3–96.0)
Straightness index	0.97 ± 0.02 (0.93–0.98)	0.85 ± 0.08 (0.7–0.94)	0.4 ± 0.18 (0.2–0.7)	0.88 ± 0.05 (0.82–0.93)

Data for each bat is from the first night only. For each bat, the "speed" was taken as the bat's median speed over the entire commuting flight, and the "altitude" as the median altitude above ground level (maximum speed and altitude were much higher). Numbers represent mean ± SD, computed over the *n* bats in each column, as well as (in parentheses) the overall range of the median speeds and altitudes for all the *n* bats. The sample size shown here includes all 36 bats used for analysis (*Methods*).

Two other types of navigational strategies should also be considered for interpreting these data: (*i*) route-based navigation and (*ii*) path integration ["dead-reckoning" (2)]. To disentangle these possibilities, we carried out homing experiments in which bats were captured in the cave and released in several remote locations outside their familiar area (*Methods*).

In the first set of homing experiments, we captured 21 bats in the same cave, equipped them with GPS dataloggers, and released them in the Negev Desert, 44 km south of the cave (Fig. 2*A*, release site R1). This location was well beyond the bats' familiar area: although the history of each individual bat before capture is unknown, it is unlikely that bats were familiar with this release site, located well outside the foraging area of all bats tracked previously from this colony ($N = 38$; Fig. 2*A*, gray polygon; *Methods*). Furthermore, fruit trees and fruit bats are scarce in this desert area (23). Sixteen of the 21 bats (76%) were found via the radiotelemetry signal in their familiar area in the same night and as long as 1 wk after release; there were no significant differences in probability of returning home as function of sex, body size, body mass, body condition, or GPS datalogger size relative to the bat (*Methods*). Analysis of full return tracks from all the retrieved GPS dataloggers ($n = 10$) showed that bats flew directly and rapidly from the release point to a specific familiar goal location (Fig. 2*B* and Table 1; straightness index, 0.85 ± 0.08). We were able to control for the particular goal location of individual bats by providing two different treatments before release (*Methods*). Six bats released late at night, after being fed ad libitum, were expected to fly to a cave; five of them did as expected (Fig. 2*A*). Four bats released early at night, without being fed, were expected to fly to their favored tree; all of them did as expected (Fig. 2 *C* and *D* show two of those bats), and also returned to the same tree night after night (Fig. 2 *C* and *D* and Fig. S5). These observations significantly match our expectations from the two treatments (Barnard exact test, $P = 0.013$).

These homing experiments further argue against olfactory beaconing to a specific tree as a potential navigational mechanism, because bats bypassed numerous similar trees (Fig. 2 *E*–*G*, black dots). They also argue against route-following and path-integration mechanisms, because such mechanisms would lead to disorientation at the unfamiliar release site R1. Our findings suggest that, similar to honeybees and pigeons (3, 15, 16), bats

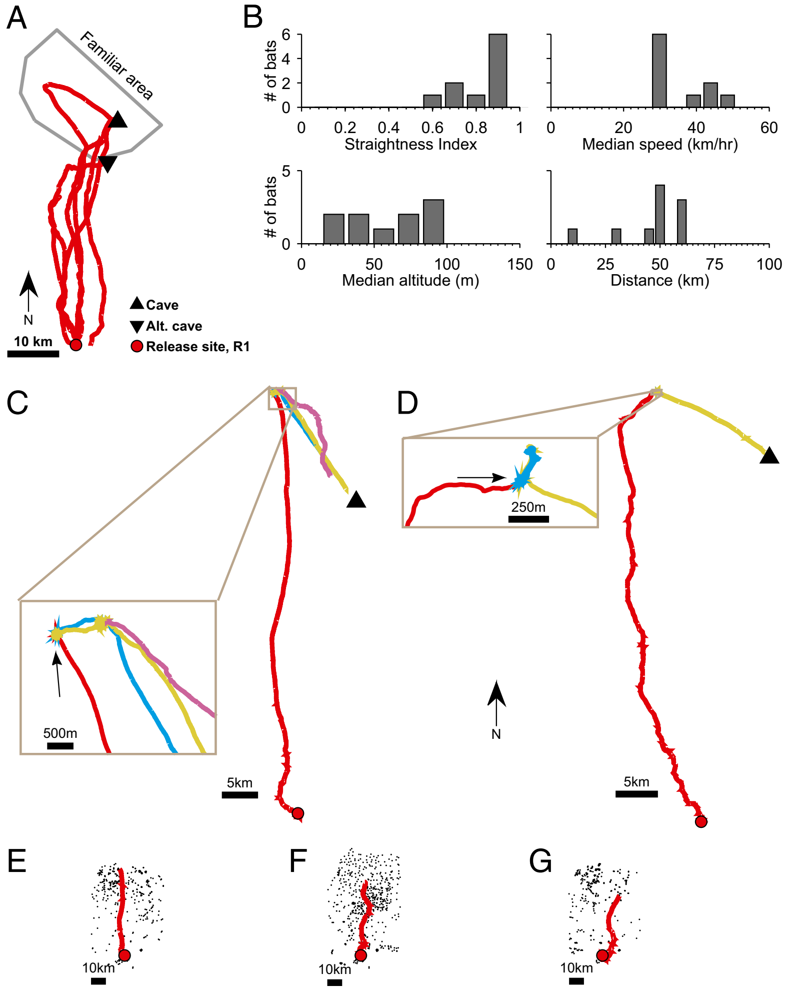


Fig. 2. Translocation experiments indicate strong homing capacity of Egyptian fruit bats. (*A*) Homing flights of all bats that homed from release site R1 directly to the cave or to a nearby alternate cave. (*B*) Flight parameters of all bats (both bats that homed to the cave as in *A* and bats that flew to trees as in *C*–*G*; $n = 10$); same notation as in Fig. 1*D*. (*C* and *D*) Examples of bats that flew from release site R1 to a tree, and then returned to the same individual tree night after night; colors represent different nights. (*C*) Bat 230 flew to a *Morus alba* tree (*Inset*, arrow) for three consecutive nights. (*D*) Bat 160 flew to a *Diospyros kaki* tree (arrow) for three consecutive nights. (*E*–*G*) Bats flew to a particular tree (and subsequently returned to the same tree night after night) while ignoring many other trees of the same species on the way (black dots). (*E*) Bat 230 flew to a *M. alba* tree. (*F*) Bat 191 flew to a *Ceratonia siliqua* tree. (*G*) Bat 232 flew to a *Eriobotrya japonica* tree.

are able to home to one of two goal locations—trees or caves—indicating flexible navigational abilities. However, these results cannot help distinguish between map-based navigation guided by large-scale odor gradients (24) or magnetic gradients (25), versus navigation using cognitive-map mechanisms relying on self-triangulation based on distal visual landmarks (26).

To further elucidate the existence of a navigational map, and to examine the role of self-triangulation based on distal visual landmarks (26), we conducted a second set of homing experiments from a larger distance. This was needed because, in the first set of homing experiments, there was considerable overlap between the visually familiar area (Fig. 3*A*, large black polygon) that can be visible by bats at the maximum flight altitude recorded within their home range (643 m above ground level) and the area visible from the highest point (115 m above ground) that was reached by a bat within 0.5 km from release point R1 (Fig. 3*A*, red dots show the line-of-sight overlap between these two locations). To test if the presence of familiar visual landmarks is necessary for large-scale navigation of bats, we repeated the same procedures but released 10 bats at point R2, 84 km from the cave, deep within a large natural erosional crater in southern Israel (Fig. 3*B*), from which familiar distal landmarks are not visible (Fig. 3*A*, no small green dots, i.e., no overlap in line of sight between point R2 and the familiar area). Nine of the 10 bats (90%) were detected in their familiar area in the same night and as long as 1 wk after release, based on radiotelemetry tracking; seven of these nine GPS devices were subsequently found (Table 1; examples in Fig. 3 *B* and *C*, green lines). As a control group, we also released 11 bats from point R3—the highest mountain at the northwestern rim of the crater, 79 km from the cave—from which familiar distal landmarks are visible (Fig. 3*A*, small blue dots denote overlap in line of sight between point R3 and the familiar area). Eight of the 11 bats (72%) were found in their familiar area in the same night and as long as 1 wk after release, based on radiotelemetry tracking; six of these eight GPS devices were subsequently retrieved, and four of them had valid data (*Methods*; examples in Fig. 3*C*, blue lines). No difference was found in the return-rate probability between bats released within the crater and control bats release on the rim (Barnard exact test, $P = 0.49$).

Bats released within the crater were fully surrounded by high cliffs, blocking the view of any familiar visual landmark; these bats typically exhibited substantial initial disorientation inside the crater (Fig. 3*B*, green), but eventually left the crater at the home direction and continued to fly north toward their cave (Fig. 3*C*, green lines). In contrast, bats released at the high crater rim,

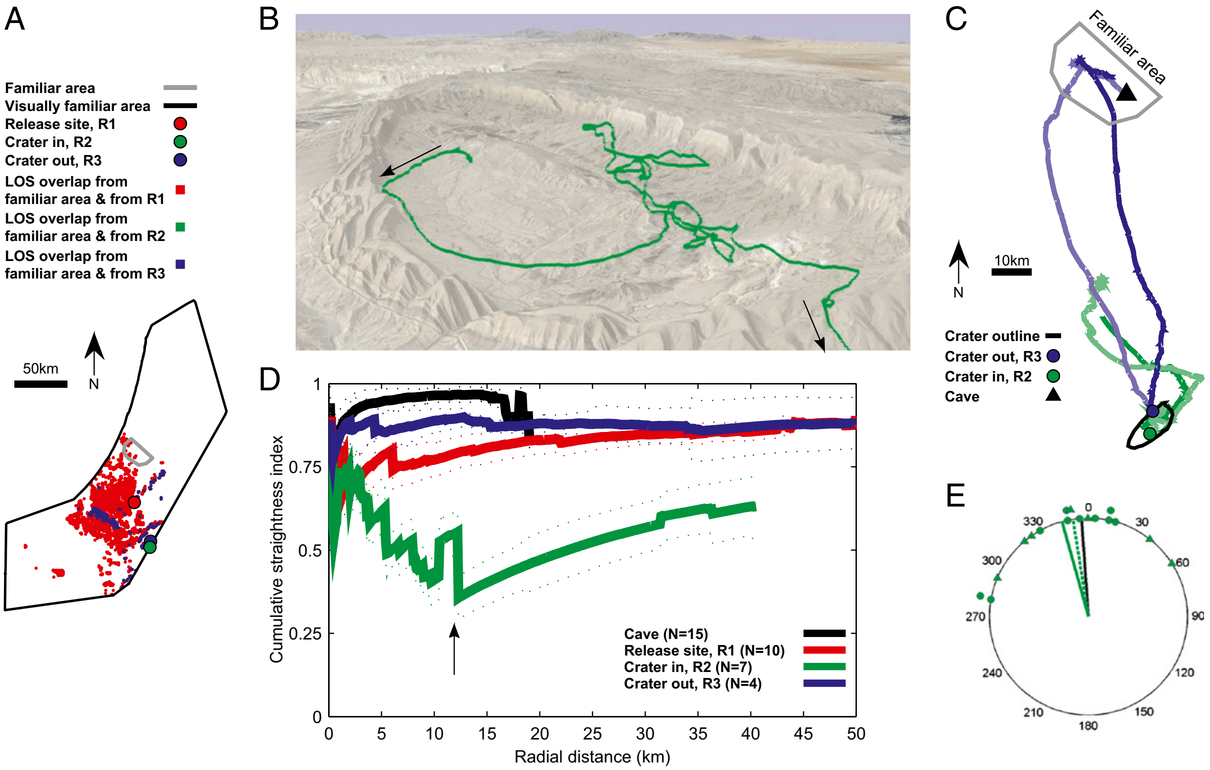


Fig. 3. Bat navigation relies primarily but not exclusively on distal visual landmarks. (*A*) Line-of-sight calculations: large black polygon represents the visually familiar area, as seen from the highest recorded altitude of bats' flights (643 m above ground level); small gray polygon represents the familiar area physically visited by foraging bats (*Methods*). Red squares mark locations seen both from the familiar area (near cave) and from release site R1 (at the highest recorded flight altitude of 115 m). Blue squares represent the same for release site R3 (at the highest flight altitude of 74 m). Note absence of green squares, indicating that bats released within the crater (R2), flying at the highest recorded altitude of 101 m, could not see any familiar visual landmarks. (*B*) Example of bat 259, released inside the crater; note the tortuous disoriented flight: this bat flew 33.9 km before it left the crater and turned northeast, then northwest toward the familiar area. View from the northeast. (*C*) Homing flight of two bats (bats 259 and 274, green lines) released inside the crater and two bats (bats 317 and 318, blue lines) released high on the crater rim; light-gray polygon represents the familiar area of the bats. Note that bats released at the crater rim flew north much straighter than bats released inside the crater. (*D*) Population data showing cumulative straightness index as function of distance from the release site; the four colors represent bats released at the four different release locations (cave, R1, R2, and R3); dotted lines represent median ± SE of the median; shown are only the distances with data from at least three bats. Note the substantially lower cumulative straightness index for within-crater releases (green), indicating strong disorientation when distal landmarks are not visible. (*E*) Polar display of bats' vanishing bearings (green circles) and the direction of the bats' exit points from the crater (triangles) after release at point R2 (inside crater). Green solid and dotted lines represent average directions of the circles and triangles, respectively; black line represents homeward direction (to cave).

only 5.6 km from the within-crater release point, flew straight north (Fig. 3*C*, blue lines). Analysis of cumulative straightness index (Fig. 3*D*) showed that bats released within the crater (Fig. 3*D*, green) flew along a considerably more torturous path compared with all other experimental bat groups. The tortuosity of their path was especially prominent at a 12-km distance (Fig. 3*D*, arrow; large decrease in straightness index), which corresponds approximately to the length scale of this crater, the size of which is 14 × 6 km, indicating that bats exhibited initial strong disorientation within the crater, and then, after they exited the crater, undertook consistent directional flight toward their familiar area. Thus, the crater release experiments clearly suggest that distal visual landmarks, such as hills or town lights, are important for large-scale homing in Egyptian fruit bats. Notably, however, all bats released at point R2 eventually left the crater at their homeward (northern) direction relative to the release point, as indicated by radiotelemetry-based vanishing bearings (Fig. 3*E*, green circles; $n = 10$ bats; mean angle, 341°; Rayleigh test, $P < 0.001$) and by GPS data of bats' exit points outside the crater walls (Fig. 3*E*, green triangles; $n = 7$; mean angle, 351°; Rayleigh test, $P = 0.011$). This suggests that visual landmarks are important but not necessary for long-range navigation by these bats. We thus propose that their long-distance homing capacity depends primarily on their ability to extrapolate their position from the geometric configuration of distal visual landmarks, coupled with at least one additional navigational mechanism—magnetic (27, 28), celestial, or olfactory-based navigation—being used when distal landmarks are not visible.

Discussion

Here we studied the navigational capacity of a flying mammal, the Egyptian fruit bat. When GPS-tagged bats were released at their cave, they exhibited high, fast, and very straight commuting flights from their cave to remote fruit trees, and returned to the same tree night after night. Bats displaced 44 km south homed directly to one of two goal locations—familiar fruit tree or cave—ruling out beaconing, route-following, or path-integration mechanisms, and providing evidence for map-like navigation in these mammals.

Previous studies of homing in bats have (*i*) demonstrated homing after several days or weeks, rather than straight rapid homing flights (29); (*ii*) demonstrated a clear beaconing strategy in bat navigation, rather than a map-like navigational strategy (30, 31); or (*iii*) released bats too close to their roost to be able to judge which navigational strategy the bats used (27). Here, we were able to overcome these shortcomings of previous studies by using GPS to precisely measure the straightness and speed of bats' flights, by releasing bats very far from their familiar area, and by performing manipulations that indicated that Egyptian fruit bats do rely on map-like navigation.

What are the sensory mechanisms used by these bats for long-range navigation? We hypothesized that the bats may use a combination of visual, magnetic, and olfactory-based navigation. To test this, we released bats inside a deep erosional crater or just outside it. Bats released within the crater were initially disoriented, but eventually left the crater toward the home direction and homed successfully, whereas bats released at the crater-edge top homed directly. The crater-release experiments indicate that visual-based navigation may be of particular importance to these bats. The differences in bats' behavior between the two release points at the crater (disorientation at release point R2 within the crater, vs. straight homing from crater-rim release point R3) are likely a result of differences in availability of visual landmarks—not to differences in celestial cues, magnetic cues, or olfactory cues. Although all these sensory mechanisms were likely used by bats to eventually exit the crater in the homeward direction (Fig. 3*E*), these mechanisms are unlikely to underlie the clear behavioral differences between the within-crater and crater-rim releases (Fig. 3*D*, green vs. blue), because of the small differences in magnetic, celestial, or olfactory information between release points R2 and R3. The behavioral differences between points R2 and R3 are unlikely to be caused by differences in exposure to celestial cues, because R2 and R3 releases were done at the same night, and no systematic differences in cloudiness were observed. The dramatic behavioral differences between points R2 and R3 are unlikely to be caused by differences in magnetic-field parameters, because of the very small distance between points R2 and R3 (5.6-km aerial distance) and the relatively small differences in magnetic parameters between the two nearby release points, R2 and R3 (magnetic maps shown in Fig. S6 and ref. 32). Finally, the dramatic behavioral differences between points R2 and R3 are not very likely to be caused by differences in olfactory cues in those two locations. Olfactory navigation, possibly cued by wind-transported odorants originating from abundant orchards at the bats' familiar area, might be plausible, in principle, as a navigational mechanism, as the typical afternoon breeze from the Mediterranean Sea reaches the study area in the Negev Desert a few hours later (33). However, we consider this mechanism unlikely to explain any behavioral differences between bats released at points R2 and R3 because all bats were in fact released on nights with no winds or very weak winds, indicating that, although the nocturnal breeze could potentially carry odorants from the foraging area, it was not likely to be very effective at the time of release. Nevertheless, further research is needed to examine the roles of these three possible mechanisms in detail. For example, it has been suggested that visual celestial cues near the horizon are important for bird navigation (5, 34), and it might be possible that the lower portion of the sky was occluded by surrounding cliffs for those bats that were released inside the crater. Furthermore, the effects of the crater's complex terrain on wind-mediated odor transport above and within the crater warrants further investigation. However, although it is possible that there was some contribution of magnetic, celestial, and olfactory navigation, the most parsimonious explanation for the dramatic behavioral differences between release point R3 (straight homing) and point R2 (disorientation) is the visual explanation: the availability of distal visual landmarks from point R3 and the lack of familiar distal visual landmarks at point R2. The importance of vision for bat homing has been suggested in several previous studies (e.g., refs. 30, 31). Notably, Egyptian fruit bats are known to have outstanding visual acuity, much better than that of almost all insectivorous bat species (35); therefore, visual-based navigation is certainly plausible in these bats—and although we cannot determine from our experiments which precise landmarks the bats used, our results suggest that the bats used some set of distal visual landmarks for long-range navigation.

In summary, we propose that Egyptian fruit bats use self-triangulation based on multiple distal visual landmarks (26) as their primary large-scale navigational mechanism. This map-based mechanism, proposed previously for rodent navigation in a water maze (20), was studied here in a free-ranging mammal at a spatial scale five orders of magnitude larger. Our study demonstrates the importance of considering all components of the new movement ecology framework (36) for understanding movement phenomena: the internal state determining the strong motivation to move to a specific destination; the motion capacity enabling bats to execute nonstop flapping flights from distant locations; their high navigation capacity—the core component investigated in this study; and the critical role of some specific external factors such as particular fruit trees and distant visual landmarks used for navigation. More specifically, our results also suggest that Egyptian fruit bats use additional navigational mechanisms—possibly based on olfactory, celestial, and/or magnetic cues—when distal landmarks are not visible. These results suggest the ability of bats to navigate within their visually familiar area based on sets of distal visual landmarks—a capacity that could be termed a form of a visually based cognitive map (2, 19). They also demonstrate bats' ability to eventually home when translocated well outside their visually familiar area—a capacity often called "true navigation" in birds and other animals (13, 14, 24, 25). To our knowledge, this is the first evidence for either of these navigational capacities in bats, and the first evidence for large-scale navigation in a free-ranging wild mammal.

Methods

Research Site and Species. We studied the navigational strategies of wild Egyptian fruit bats (*R. aegyptiacus*) from a relatively large colony at the Sgafim cave (location, 31° 40′ N; 34° 54′ E; altitude, 250 m above sea level), located at the Judean lowlands of central Israel; the number of bats in this cave was counted yearround, and was between 400 and 800 individuals. Bats were captured by mist nets upon exiting the cave after sunset, and were kept in a cloth bag until handling. Each bat was sexed and measured for mass and forearm length, a measure of body size. For the GPS tracking experiments, we used a total of 70 adult individuals of both sexes (46 male, 24 female). We used only relatively large bats with body mass of more than 130 g (mean mass ± SD, 150.3 ± 13.8 g; forearm length, 94.6 ± 2.1 mm). Although there was a significant difference in body mass between sexes, no significant difference in any of the flight parameters was found between the sexes; hence, we pooled data from both sexes. In each night, we GPS-tagged and released between one and five individual bats. Experiments were carried out between January 2008 and December 2009; they spanned all seasons, a variety of weather conditions, and all possible moon phases. Experimental procedures were approved by the Israel Nature and Parks Authority and by the institutional animal care and use committees of the Hebrew University of Jerusalem and the Weizmann Institute of Science.

GPS Tracking Device. Adult Egyptian fruit bats (*N* = 70) were equipped with a tracking device that included a lightweight GPS datalogger (GiPSy2; Technosmart) plus a radiotelemetry unit (BD-2; Holohil Systems). The average weight of the GPS/radiotelemetry combined pack was 10.9 ± 1.3 g (range, 6.9–13.0 g), including batteries and protective casing. This weight constituted 7.3 ± 1.0% of the bats' body mass (range, 4.0–9.6%). The dimensions of the GPS/radiotelemetry pack were 48 mm (length) × 23 mm (width) × 11 mm (height).

Device Attachment and Marking of Individual Bats. Medical skin adhesive (Liquid Bonding Cement; Torbot Group) was used to attach the GPS device to the bat's back, directly above the center of mass of the animal's body. The bat was implanted with a s.c. radiofrequency identification tag for individual identification (Mini-Transponder; UNO Roestvastaal) to verify that all tracked bats were indeed distinct individuals.

GPS Sampling Rate and Time Extent of Data Collection. The mass and size of the GPS battery limited the device's lifetime, and therefore we modified the GPS sampling rate and activation schedule according to experimental needs, to collect more data. For 66 of the 70 bats, data were collected at high sampling rates (0.1–1 Hz), with most of these data (63 of 66 bats; 95.5%) collected at 1 Hz. The GPS devices were programmed to be active all night and inactive during the day (when bats were inside the cave). Additionally, in some cases, the GPS was activated for only the first part of the night; this saved battery power and allowed GPS recording of bats' movements for as many as four consecutive nights. Total time extent of data collection ranged from full sampling over one night to 3 h of data per night over as many as four consecutive nights. All bats were also tracked manually by standard radiotelemetry triangulation for purposes of GPS retrieval (typically this tracking was conducted for the first one or two nights after release, and then was intermittently conducted over the following several weeks).

Bat Release. Before release, bats were given a few milliliters of fruit juice to prevent dehydration and stress related to capture. To prevent group navigation of our experimental bats, we released the bats only after all other bats left the cave (for bats released near the cave), and if several bats were tagged and released on the same night, we released them individually at intervals of more than 20 min. Before release, bats were rotated several times and released from the hand at a random direction.

Homing Experiments. For homing experiments, we used the same capture and attachment protocol as with cave-released bats. We carried out three sets of homing releases in the Negev Desert, releasing the bats at the following locations: (*i*) release site R1, Gva'ot Goral (aerial distance of 44 km from capture site; 31° 17′ N; 34° 49′ E; altitude 419 m above sea level); (*ii*) release site R2, inside HaMakhtesh HaGadol natural erosional crater (aerial distance of 84.5 km from capture site; 30° 55′ N; 34° 58′ E; altitude 400 m above sea level); and (*iii*) release site R3, outside of HaMakhtesh HaGadol crater (aerial distance of 79 km from capture site; 30° 58′ N; 34° 58′ E; altitude 638 m above sea level). Translocation was done by car, driving the bats total ground distances of 58, 111, and 105 km, respectively. During the entire transport, bats were held inside a cloth bag.

For the release in Gva'ot Goral (site R1), upon arrival to the release location, bats were randomly assigned to one of two treatment groups: (*i*) 11 bats were released immediately and 10 bats were kept in a closed cage for at least 3 h, given fruits and water ad libitum as well as fed by hand, and only then released (~3 h before sunrise). For the inside- and outside-crater releases (sites R2 and R3), bats were held in a cloth bag during the drive to the release site, with ad libitum food provided; upon arrival to the site, the bats were released by using the same protocol.

GPS Recovery and Data Download. GPS/radiotelemetry packs were retrieved after the pack had fallen to the ground (usually after a few weeks). Retrieval of the GPS unit was done by using the radiotelemetry signal. Data download was possible only by physically retrieving the device. In total, we retrieved 51 of the 70 GPS devices (73%) that we deployed. Retrieval rates were 89.3%, 61.9%, 70.0%, and 54.5% for bats released at the cave and sites R1, R2, and R3, respectively. GPS tags of translocated bats (released at R1, R2, or R3) had significantly lower retrieval rates than those of nontranslocated bats released at the cave (χ^2 = 6.37, df = 1, *P* = 0.012). However, there was no significant difference in retrieval success among the three groups of translocated bats (χ^2 = 0.531, df = 2, *P* = 0.767). Therefore, we expect no bias related to tag retrieval success among the three experimental treatments.

Inclusion Criteria for Analysis. Of the 51 bats whose GPS/radiotelemetry packs were retrieved, we excluded four (three released at the cave and one at R1) that had corrupted data, and two tags (released at R3) that had partial data collected during only a portion of their track as a result of technical failure. Because statistical properties estimated for the same movement path might differ if data points are collected at different sampling rates (37), we narrowed the range of sampling rates by excluding four additional bats, all released at the cave, whose GPS locations were recorded at low sampling rates of approximately 0.017 Hz. Data from five additional bats, three released at the cave and two at R1, were excluded because those bats flew to a fruit tree near (<5 km) the release point and stayed there several hours. We note that the two bats from R1 must have eventually commenced long-distance (unrecorded) homing flights, because their radio signal was detected at the cave on the following morning. The remaining 36 bats formed the basic dataset for all analyses (Table 1). Subcutaneous identification tags verified that all bats were distinct individuals. Of those 36 bats, 21 bats had single-night data, whereas six, seven, and two bats had two, three, and four nights of data, respectively, resulting in a total of 62 nights from 36 bats.

Considering all lost tags and exclusions, the proportion of individuals contributing data to the analyses was not significantly different between translocated and nontranslocated bats (χ^2 = 0.008, df = 1, *P* = 0.931) or among the three groups of translocated bats (χ^2 = 2.377, df = 2, *P* = 0.305). The latter comparison means that there were no differences in data exclusion or tag retrieval success between the three groups of translocated bats, released at sites R1, R2, and R3; this is important because a key comparison in the current study is among the bat groups released at sites R1, R2, and R3: hence, we expect no bias among these three treatments in relation to data exclusion or tag retrieval success.

Data Analysis. For each bat, we included only data points that had high accuracy, by including only individual points that were based on (*i*) at least four satellites and (*ii*) positional dilution of precision less than 12 (this is a standard parameter that quantifies how well the GPS satellites span the sky, which influences the reliability of the GPS reading; see ref. 38).

GPS tracks were segmented into "flight" and "nonflight" portions. A flight segment was defined as a segment in which the bat flew with a ground speed of more than 10 km/h for more than 20 s; all other segments were defined as nonflight. If two flight segments were separated with a nonflight segment whose duration was shorter than 10 min, the two flight segments were merged together.

For all the individual commuting flights, we computed the following trajectory data: (*i*) altitude above ground level; (*ii*) flight speed; (*iii*) total flight distance; (*iv*) straightness index [defined as *D*/*L*, where *D* is the length of the straight line from the starting-point to the goal and *L* is the actual total length of the segment flown (39)]; and (*v*) "first tree stop," defined as the first stop by the bat at a tree that lasted longer than 10 min; we also physically inspected all the stop locations to identify the tree species and evaluate their fruiting status.

All data analyses of bat trajectories were done by using Matlab (Mathworks). Ground elevation was extracted from a digital terrain model layer with cell size of 25 m^2 (created by J. K. Hall, Geological Survey of Israel, Jerusalem, Israel). Statistical tests were done by using the SPSS statistical software (version 17; SPSS); all test results were considered significant if $P < 0.05$.

The familiar area of the bats (Figs. 2*A* and 3 *A* and *C*, gray polygon) was computed as the 95% convex hull encompassing the positional data from all GPS releases at the cave ($n = 19$ bats; we included for this particular analysis also GPS data with low sampling rate < 0.1 Hz), as well as positional data from additional foraging bats that were tracked with only radiotelemetry ($n = 19$)—a total of 38 individual bats, recorded over all seasons.

For line-of-sight calculations, in addition to the familiar area, we computed the visually familiar area, which is based on the notion that, when flying very high up, bats could see visual landmarks from very long distances, and thus may learn the layout of landmarks over a much larger area than the area they physically visited (26). We calculated the visually familiar area (Fig. 3*A*, large black polygon) by conducting line-of-sight calculation from 100 randomly selected points within the familiar area, at an altitude of 643 m above ground level, which is the highest altitude recorded for foraging bats. The line-of-sight calculation was done by using a digital terrain map with a cell size of 1 km^2 (digital terrain map raster file; created by J. K. Hall, Geological Survey of Israel, Jerusalem, Israel), resulting in the large visually familiar area shown by the black polygon in Fig. 3*A*. A line-of-sight calculation was also done for the translocation release site R1 in the Negev Desert (at an altitude of 115 m above ground level, which is the highest altitude recorded for a translocated bat within 0.5 km distance from release site R1). Red squares in Fig. 3*A* show the overlap between these two line-of-sight calculations: that is, the locations that could be seen by bats both from their familiar area and from release site R1. This calculation confirmed that many visual landmarks could indeed be seen from both locations, despite the large translocation distance (aerial distance of 44 km). Similar calculations were done for release sites R2 and R3 (at altitudes of 101 m and 74 m above ground level, respectively, the highest altitude recorded for translocated bats within 0.5 km distance from release sites R2 and R3, respectively). The blue squares in Fig. 3*A* show the locations that could be seen by bats from both their familiar area and release site R3, showing that bats released at site R3 (a high mountain on the crater edge) could potentially use visual landmarks to navigate. Note that, in contrast, there are no green squares in Fig. 3*A*, that is, there are no locations that could be seen both from the familiar area and from release site R2, which means that bats released at site R2 (within the crater) could not see any familiar visual landmarks.

Cumulative straightness index (Fig. 3*D*) was calculated for all tracks as follows. For each radial distance *l* from the release point, we computed the straightness index (as detailed earlier) by using the flight segment that starts at the release location and ends at the first point on the bat's trajectory at which the distance from the release location exceeded *l*. The cumulative straightness index was computed in 100-m intervals (i.e., *l* was set to 100, 200, 300 m. . . up to 50 km; *l* is shown on the *x* axis of Fig. 3*D*).

ACKNOWLEDGMENTS. We thank K. Cheng, J. Zeil, A. Nirendra, T. Kimchi, T. Merkle, M. Arbib, N. Sapir, W. Wiltschko, and R. Wiltschko for helpful discussions; O. Altstein, D. Shohami, A Zabari, and Y. Yovel for technical assistance in the field; and A. Ben-Nun (GIS Center, Hebrew University) and N. Horvitz for technical assistance in spatial analysis of the data. This study was funded by Israel Science Foundation (ISF) Grants ISF-FIRST 1316/05 and ISF 1259/09 (to R.N.); the Adelina and Massimo Della Pergolla Chair of Life Sciences (R.N.); Forschungskredit Universität Zürich (A.V.); *Ornis italica* (G.D.); research grants from the Carl and Micaela Einhorn-Dominic Brain Research Institute, Nella and Leon Benoziyo Center for Neurological Diseases, and Mr. and Mrs. Steven Harowitz (N.U.); and fellowships of Bat Conservation International, the Lubee Bat Conservancy, the Zoological Society of Israel, and the Rieger–Jewish National Fund Foundation (A.T.).

---

1. Wallraff HG (2005) *Avian Navigation: Pigeon Homing as a Paradigm* (Springer, New York).
2. Gallistel CR (1990) *The Organization of Learning* (MIT Press, Cambridge, MA).
3. Menzel R, et al. (2005) Honey bees navigate according to a map-like spatial memory. *Proc Natl Acad Sci USA* 102:3040–3045.
4. Lohmann KJ, Lohmann CM, Ehrhart LM, Bagley DA, Swing T (2004) Animal behaviour: geomagnetic map used in sea-turtle navigation. *Nature* 428:909–910.
5. Cochran WW, Mouritsen H, Wikelski M (2004) Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* 304:405–408.
6. Ritz T, Thalau P, Phillips JB, Wiltschko R, Wiltschko W (2004) Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature* 429:177–180.
7. Srinivasan MV, Zhang S, Altwein M, Tautz J (2000) Honeybee navigation: Nature and calibration of the "odometer". *Science* 287:851–853.
8. Biro D, Freeman R, Meade J, Roberts S, Guilford T (2007) Pigeons combine compass and landmark guidance in familiar route navigation. *Proc Natl Acad Sci USA* 104: 7471–7476.
9. Thorup K, et al. (2007) Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. *Proc Natl Acad Sci USA* 104:18115–18119.
10. Graham P, Cheng K (2009) Ants use the panoramic skyline as a visual cue during navigation. *Curr Biol* 19:R935–R937.
11. Kramer G (1953) Die sonnenorientierung der vögel. *Verh Dtsch Zool Ges* 1:77–84.
12. Perdeck AC (1958) Two types of orientation in migrating starlings, Sturnus vulgaris and chaffinches, Fringilla coelebs, as revealed by displacement experiments. *Ardea* 46:1–37.
13. Boles LC, Lohmann KJ (2003) True navigation and magnetic maps in spiny lobsters. *Nature* 421:60–63.
14. Phillips JB, Adler K, Borland SC (1995) True navigation by an amphibian. *Anim Behav* 50:855–858.
15. Lipp H-P (1996) "Columba militaris helvetica": *Biologie und Verhaltensleistungen der Schweizerischen Armeebrieftauben* [Biology and spatial behavior of homing pigeons in the Swiss army]. *Acta Biol Benrodis*, 3(Suppl):85–103 (in German).
16. Baldaccini NE, Benvenuti S, Fiaschi V (1976) Homing behaviour of pigeons confined to a new loft distant from their home. *Monitore Zool Ital* 10:461–467.
17. Lipp H-P, et al. (2004) Pigeon homing along highways and exits. *Curr Biol* 14: 1239–1249.
18. Tolman EC (1948) Cognitive maps in rats and men. *Psychol Rev* 55:189–208.
19. O'Keefe J, Nadel L (1978) *The Hippocampus as a Cognitive Map* (Oxford Univ Press, Oxford).
20. Morris RG, Garrud P, Rawlins JN, O'Keefe J (1982) Place navigation impaired in rats with hippocampal lesions. *Nature* 297:681–683.
21. Bennett AT (1996) Do animals have cognitive maps? *J Exp Biol* 199:219–224.
22. Ulanovsky N, Moss CF (2008) What the bat's voice tells the bat's brain. *Proc Natl Acad Sci USA* 105:8491–8498.
23. Mendelssohn H, Yom-Tov Y (1999) *Fauna Palaestina: Mammalia of Israel* (Israel Academy of Sciences and Humanities, Jerusalem).
24. Wallraff HG (2004) Avian olfactory navigation: Its empirical foundation and conceptual state. *Anim Behav* 67:189–204.
25. Wiltschko R, Wiltschko W (2003) Avian navigation: From historical to modern concepts. *Anim Behav* 65:257–272.
26. Baker RR (1984) *Bird Navigation: The Solution of a Mystery?* (Holmes and Meier, New York).
27. Holland RA, Thorup K, Vonhof MJ, Cochran WW, Wikelski M (2006) Navigation: Bat orientation using Earth's magnetic field. *Nature* 444:702.
28. Holland RA, Borissov I, Siemers BM (2010) A nocturnal mammal, the greater mouse-eared bat, calibrates a magnetic compass by the sun. *Proc Natl Acad Sci USA* 107: 6941–6945.
29. Davis R (1966) Homing performance and homing ability in bats. *Ecol Monogr* 36: 201–237.
30. Williams TC, Williams JM (1967) Radio tracking of homing bats. *Science* 155: 1435–1436.
31. Williams TC, Williams JM, Griffin DR (1966) The homing ability of the neotropical bat Phyllostomus Hastatus, with evidence for visual orientation. *Anim Behav* 14:468–473.
32. Shirman B (2000) Three component magnetic anomaly maps of Israel. *Isr J Earth Sci* 49:1–7.
33. Goldreich Y (2003) *The Climate of Israel: Observation, Research, and Application* (Plenum, New York).
34. Muheim R, Moore FR, Phillips JB (2006) Calibration of magnetic and celestial compass cues in migratory birds—a review of cue-conflict experiments. *J Exp Biol* 209:2–17.
35. Heffner RS, Koay G, Heffner HE (1999) Sound localization in an Old-World fruit bat (Rousettus aegyptiacus): acuity, use of binaural cues, and relationship to vision. *J Comp Psychol* 113:297–306.
36. Nathan R, et al. (2008) A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci USA* 105:19052–19059.
37. Bovet P, Benhamou S (1988) Spatial analysis of animal's movements using a correlated random walk model. *J Theor Biol* 131:419–433.
38. Kaplan ED, Hegarty CJ (2006) *Understanding GPS: Principles and Applications* (Artech House, Boston).
39. Benhamou S (2004) How to reliably estimate the tortuosity of an animal's path: Straightness, sinuosity, or fractal dimension? *J Theor Biol* 229:209–220.

Supporting Information

Tsoar et al. 10.1073/pnas.1107365108

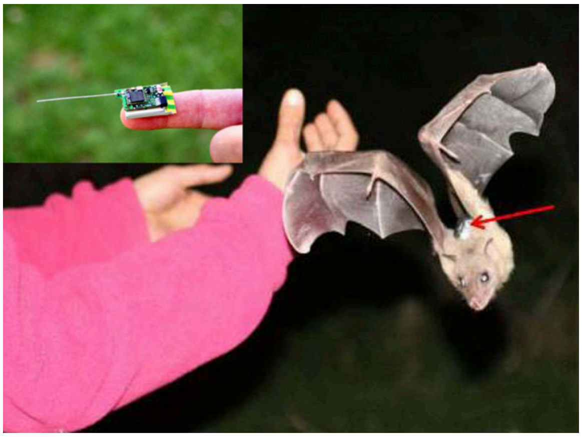


Fig. S1. GPS/radiotelemetry pack placed on the back of an Egyptian fruit bat (*R. aegyptiacus*). Photo taken at the moment of release. Photo credit: A. Tsoar. *Inset*: GPS datalogger without the radiotelemetry unit and the protective casing.

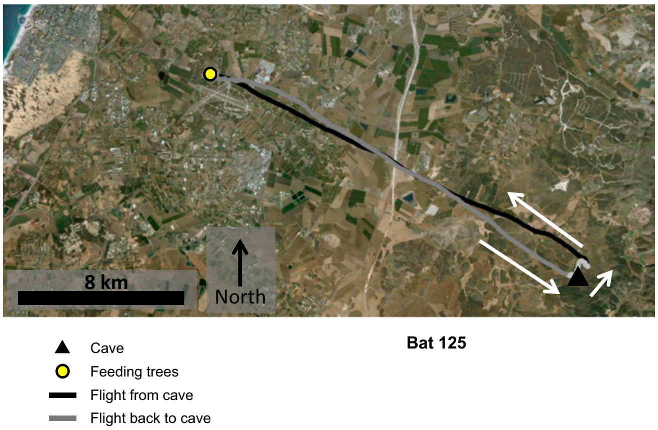


Fig. S2. Very straight commuting flights by the same bat shown in Fig. 1*A* (bat 125). The bat left the cave, flew locally (light gray line), then took a long commuting flight (black line) to the feeding trees and then commuted back to the cave (dark gray line). Superimposed on an aerial photo of the area, taken from Google Earth.

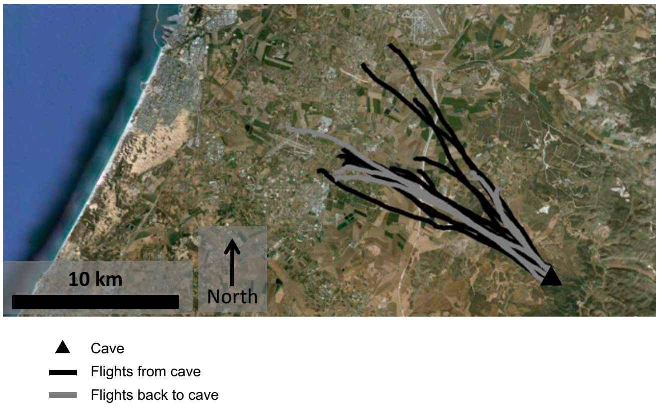


Fig. S3. Population data shows commuting flights that started or ended directly at the cave. Colors represent the long commuting flight to the feeding tree (black) or back to the cave (dark gray). Superimposed on an aerial photo of the area, taken from Google Earth. Same data as in Fig. 1*C*. Note the very straight commuting flights from the cave and back to the cave.

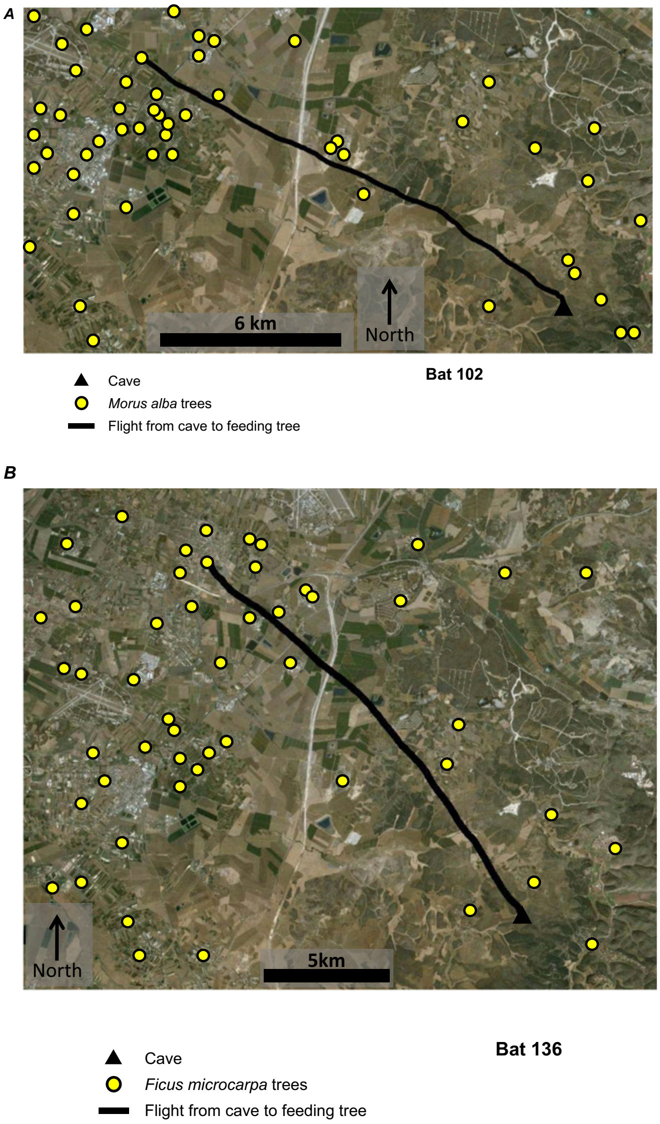


Fig. S4. Flight path to the foraging area of bat 102 (*A*) and bat 136 (*B*): these bats ignored all the plantations and individual trees of the same species on their way (*M. alba* and *Ficus microcarpa* trees, respectively). Conspecific trees and plantations are denoted here by yellow dots; note that these yellow dots correspond to the conspecific trees we were able to locate, and hence they represent a conservative estimate of all these trees in the area—the complete set of conspecific trees is certainly larger than this. Black line indicates flight trajectory superimposed on an aerial photo of the area, taken from Google Earth. These examples suggest that the bats did not use olfactory beaconing toward a specific tree to find their favored trees.

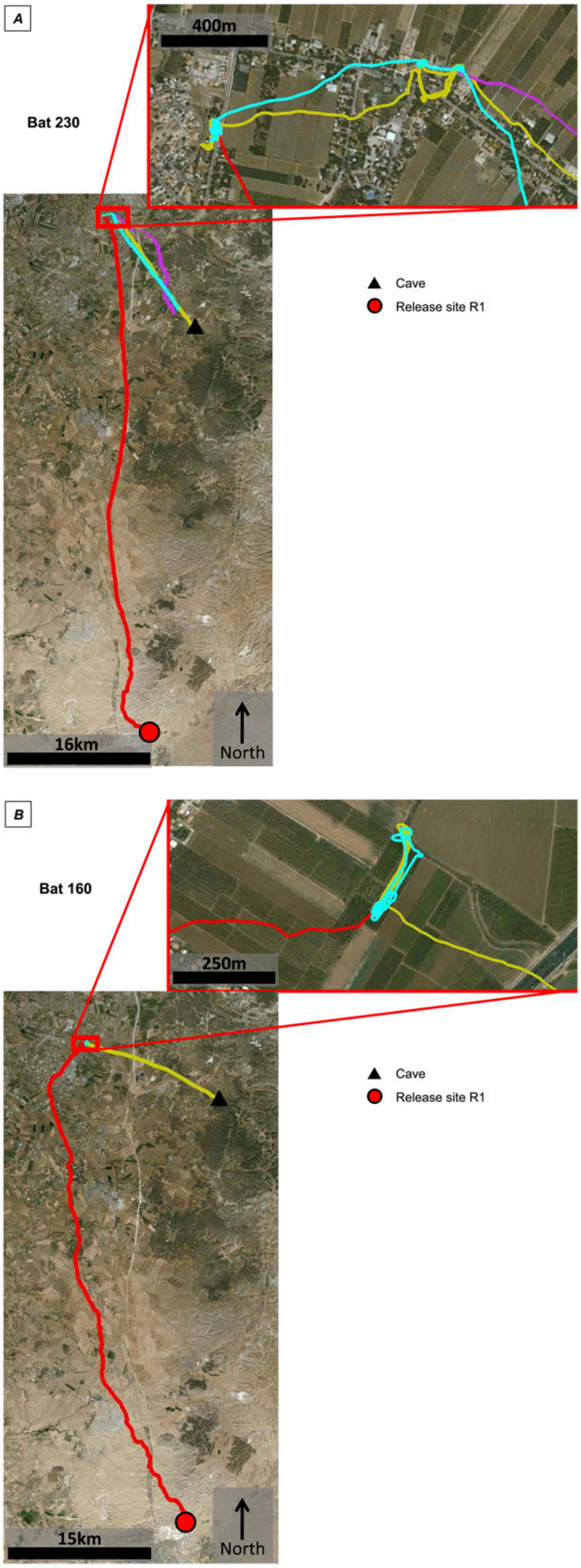


Fig. S5. Bats released at site R1 early in the night and not fed by the experimenters flew to feed at a favored tree, and then returned to the same individual tree night after night. Shown is a close-up of the foraging of a translocated bat returning to the same foraging tree on three consecutive nights (*A*, bat 230; *B*, bat 160). These are the same bats as in Fig. 2 *C* and *D*. Superimposed on an aerial photo of the area from Google Earth; different colors represent different consecutive nights.

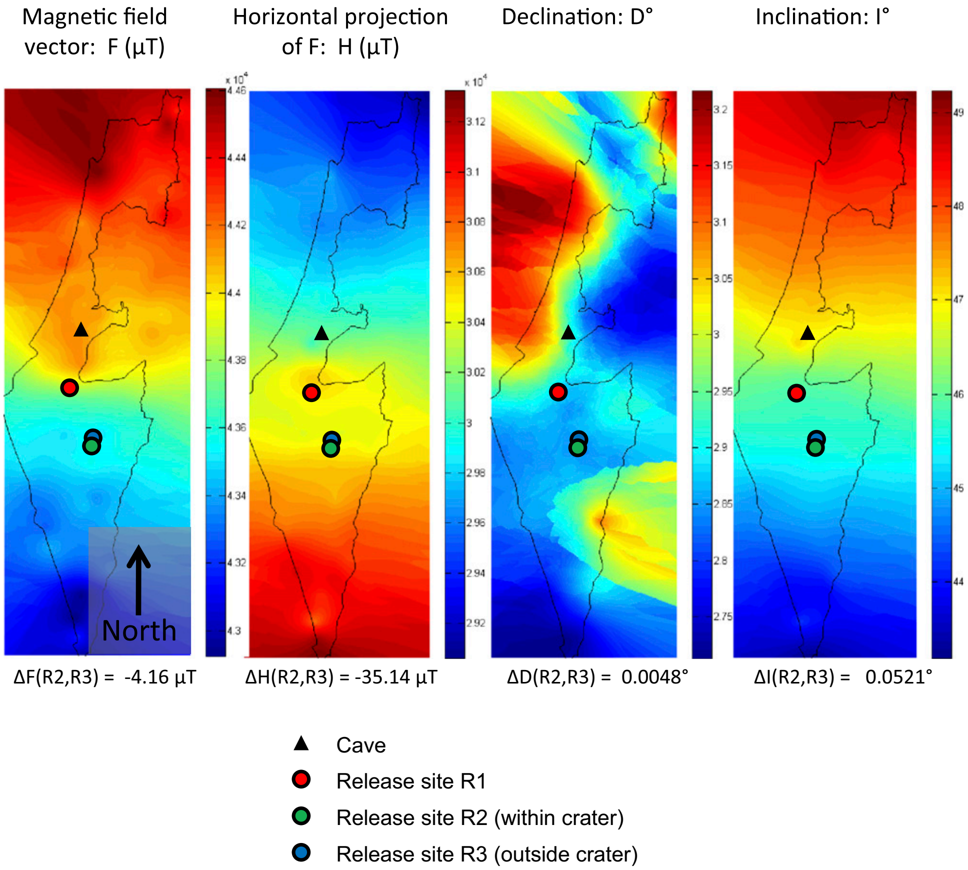
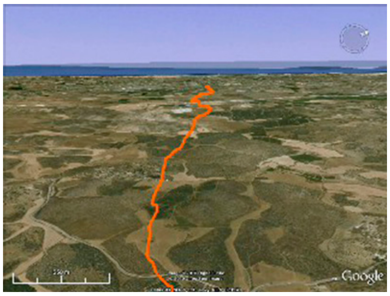


Fig. S6. Maps of four magnetic parameters show very small differences in the magnetic field between release sites R2 and R3. *F*, magnetic field vector; *H*, horizontal projection of *F*; *D*, declination; *I*, inclination. All four release sites that were used in our experiments (cave, R1, R2, and R3) are marked as well. Black contour represents national borders. Data courtesy of B. Shirman (1).

1. Shirman B (2000) Three component magnetic anomaly maps of Israel. *Isr J Earth Sci* 49:1–7.



Movie S1. Foraging flight of bat #146 from the cave to the first feeding tree. Note the very straight flight to the feeding-tree, and then the long bout of foraging at the tree.

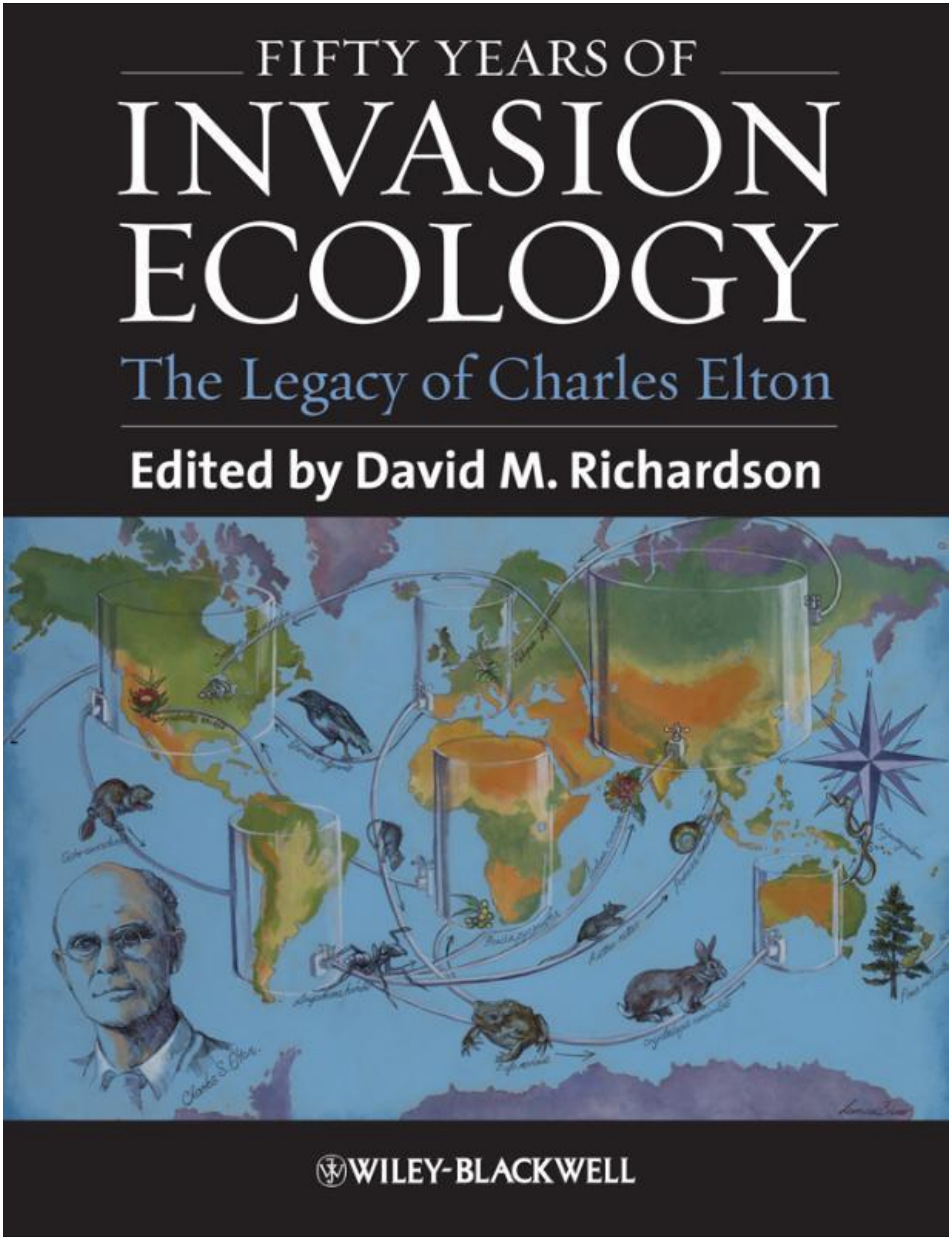
Movie S1

CHAPTER 3

A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats

Book Chapter:

Tsoar A., Shohami D. and Nathan, R. (2011) A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. In: *Fifty Years of Invasion Ecology* (Richardson DM, ed.). Wiley-Blackwell.



FIFTY YEARS OF
INVASION
ECOLOGY
The Legacy of Charles Elton

Edited by David M. Richardson

WILEY-BLACKWELL

Part 4

The Nuts and Bolts of Invasion Ecology

Fifty Years of Invasion Ecology: The Legacy of Charles Elton Edited by David M. Richardson

ISBN: 978-1-444-33585-9

Chapter 9

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

Asaf Tsoar, David Shohami and Ran Nathan

Movement Ecology Laboratory, Department of Ecology, Evolution, and Behavior,
Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem,
Jerusalem 91904, Israel

Fifty Years of Invasion Ecology: The Legacy of Charles Elton Edited by David M. Richardson

ISBN: 978-1-444-33585-9

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 manmade 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

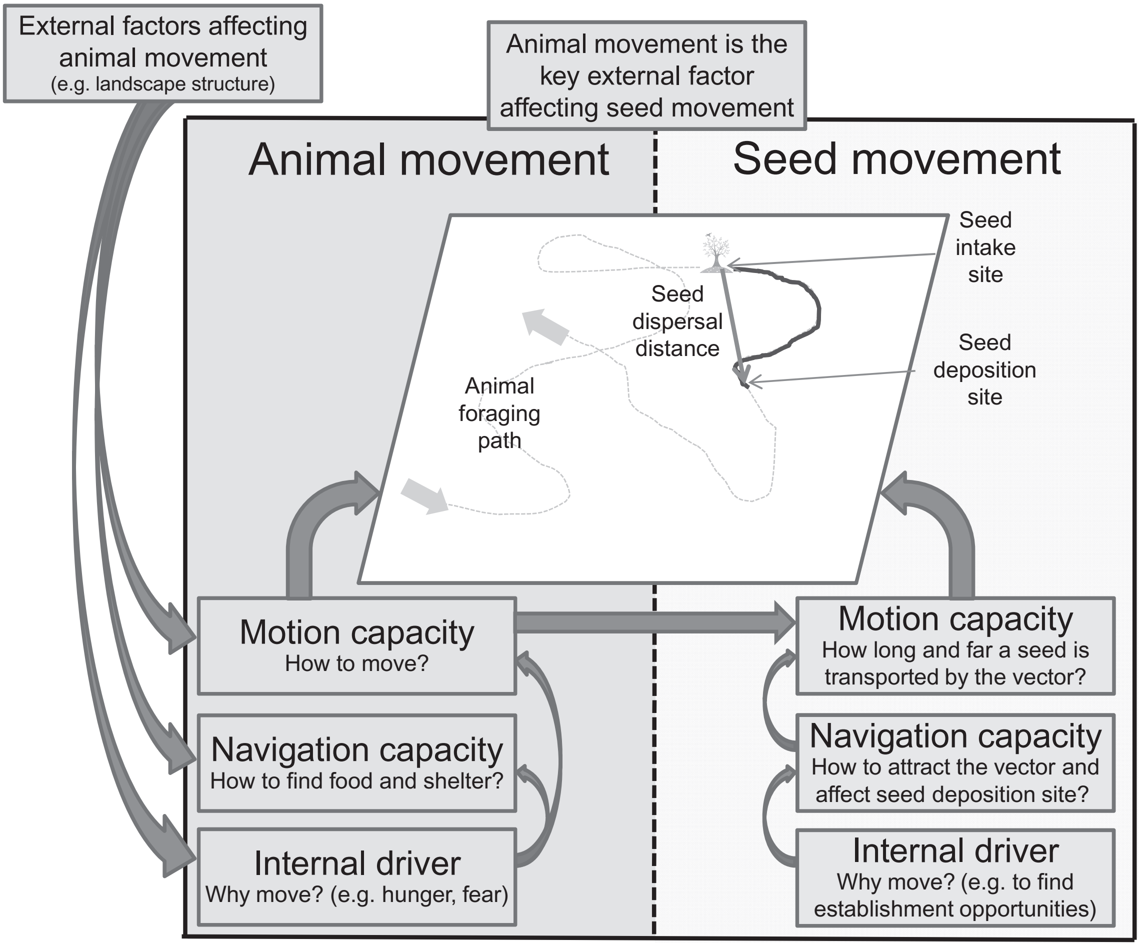


Fig. 9.1 A general conceptual framework for movement ecology of animal-dispersed plants. The framework has a twofold nested design (see main text). In the inner loop, the dispersed seed is the focal individual and the animal (the dispersal vector) is the major external factor affecting its movement.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

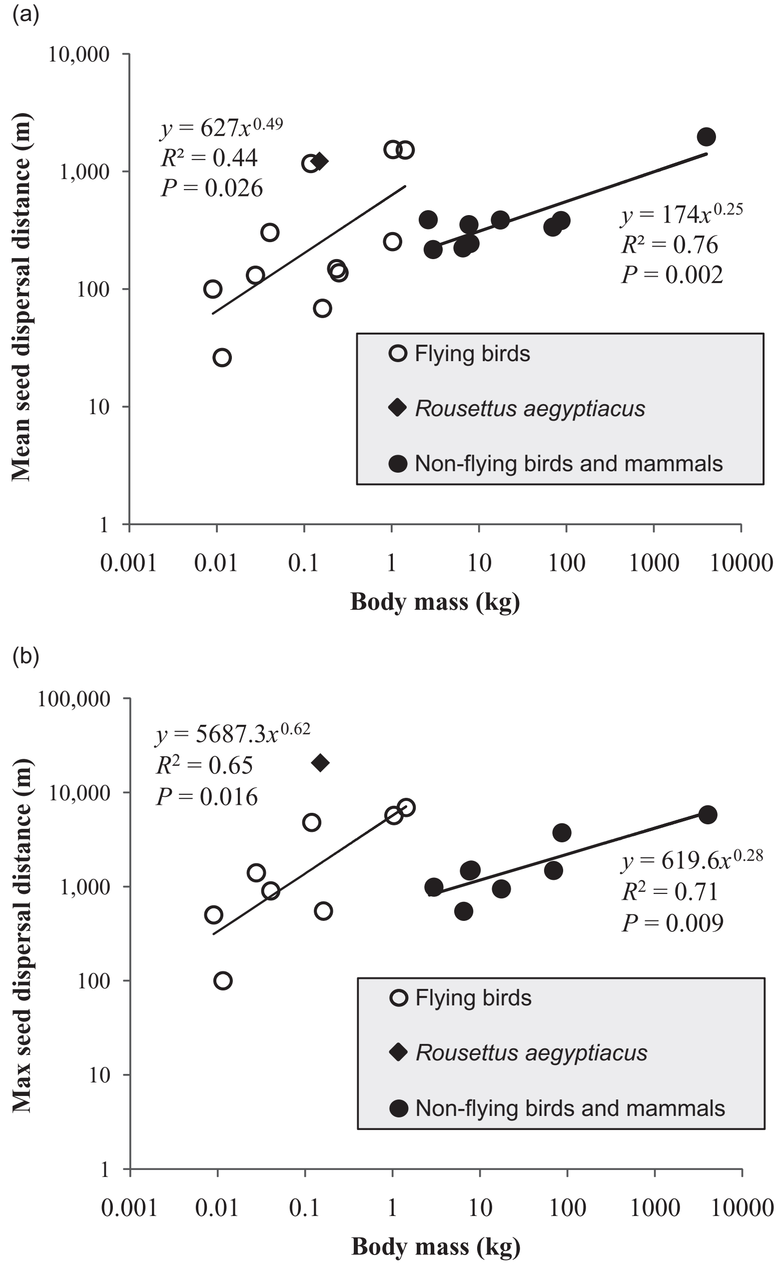
could assist in identifying invasion filters and pointing out candidate elements for management plans (Buckley et al. 2006).

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



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

$$\mathrm{GRT(h)} = 1.6\mathrm{BM}_{(\mathrm{kg})}^{0.33} \quad \text{(Robbins 1993)} \qquad (1)$$

and

$$\mathrm{SM(m/s)} = 15.7\mathrm{BM}_{(\mathrm{kg})}^{0.17} \quad \text{(Calder 1996)} \qquad (2)$$

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 ± 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 distribution 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-

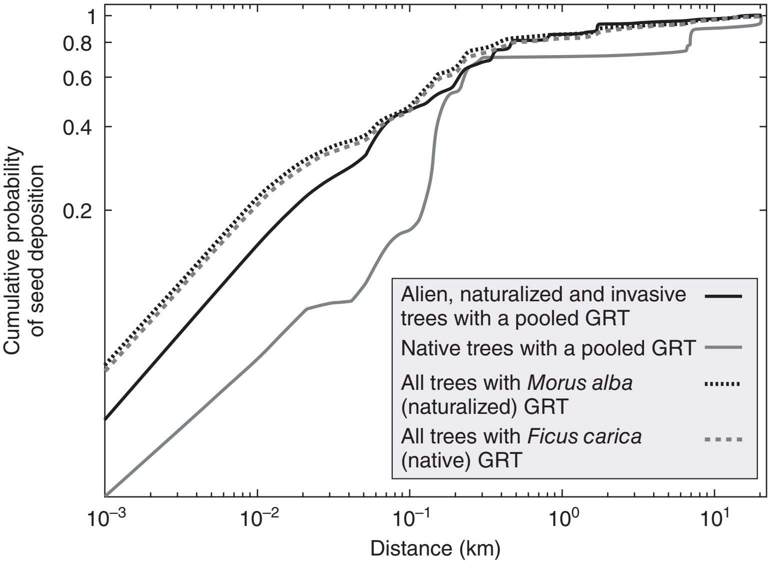


Fig. 9.2 Dispersal distance kernels of bat-dispersed seeds: the cumulative probability of seed deposition, calculated separately for the alien, naturalized and invasive tree species group (*Ficus sycomorus*, *Morus alba*, *Melia azedarach*, *Phoenix dactylifera* and *Washingtonia* sp., solid black line) 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

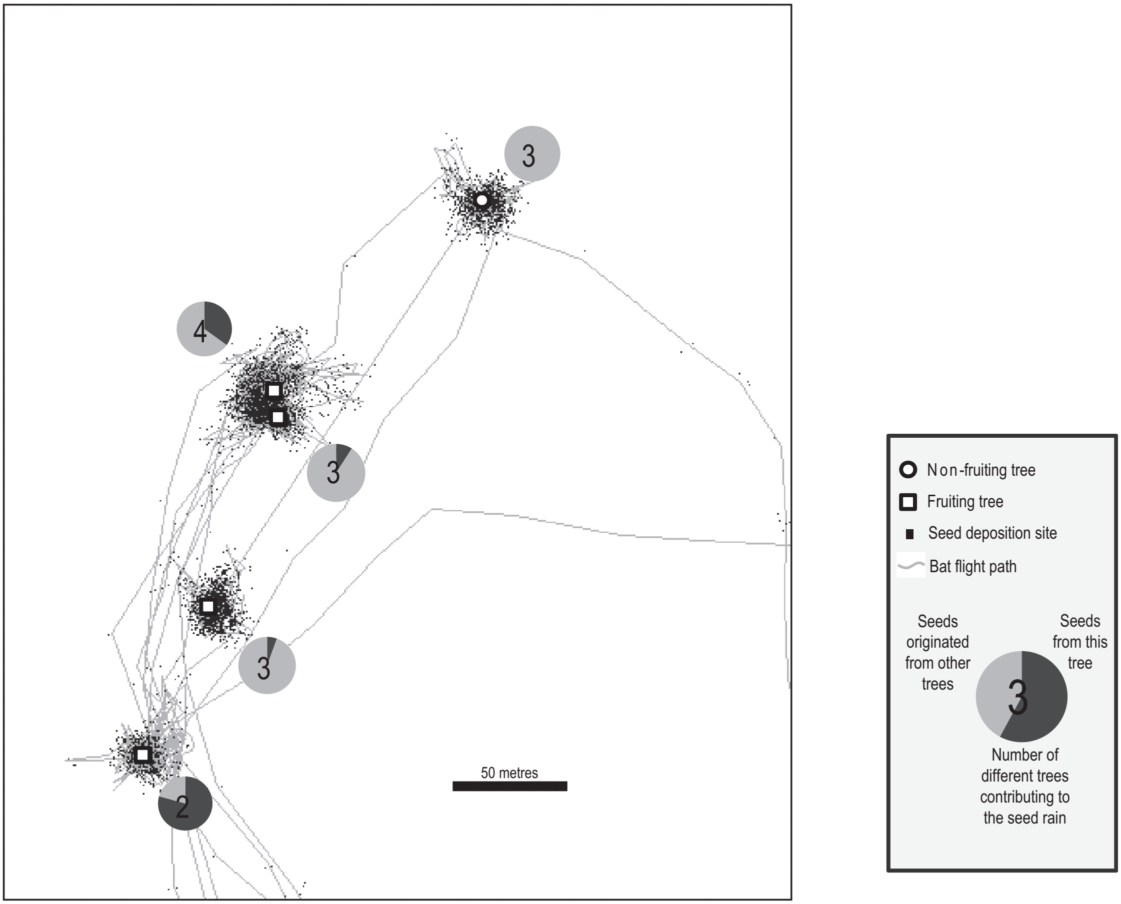


Fig. 9.3 An example of overlapping seed shadows (black dots) predicted for a full nightly path of a foraging bat (grey lines). The pie charts portray the proportions of seeds deposited in a radius of 10 m around a tree that have originated from this tree (dark grey) or from other trees (light grey). 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.

REFERENCES

Bascompte, J., Jordano, P. & Olesen, J.M. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, **312**, 431–433.

Ben-Eliahu, M.N. & ten Hove, H.A. (1992) Serpulids (Annelida: Polychaeta) along the Mediterranean coast of Israel: new population build-ups of Lessepsian migrants. *Israel Journal of Zoology*, **38**, 35–53.

Bohrer, G., Katul, G.G., Nathan, R., Walko, R.L. & Avissar, R. (2008) Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. *Journal of Ecology*, **96**, 569–580.

Broquet, T. & Petit, E.J. (2009) Molecular estimation of dispersal for ecology and population genetics. *Annual Review of Ecology Evolution and Systematics*, **40**, 193–216.

Buckley, Y.M., Anderson, S., Catterall, C.P., et al. (2006) Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology*, **43**, 848–857.

Bullock, J.M. & Clarke, R.T. (2000) Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia*, **124**, 506–521.

Bullock, J.M., Kenward, R.E. & Hails, R. (eds) (2002) *Dispersal Ecology: The 42nd Symposium of the British Ecological Society*. Blackwell, Malden.

Bullock, J.M., Shea, K. & Skarpaas, O. (2006) Measuring plant dispersal: an introduction to field methods and experimental design. *Plant Ecology*, **186**, 217–234.

Burczyk, J., Adams, W.T., Birkes, D.S. & Chybicki, I.J. (2006) Using genetic markers to directly estimate gene flow and reproductive success parameters in plants on the basis of naturally regenerated seedlings. *Genetics*, **173**, 363–372.

Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany*, **87**, 1217–1227.

Calder, W.A. (1996) *Size, Function and Life History*, 2nd edn. Dover Publications, New York.

Campos-Arceiz, A., Larrinaga, A.R., Weerasinghe, U.R., et al. (2008) Behavior rather than diet mediates seasonal differences in seed dispersal by Asian elephants. *Ecology*, **89**, 2684–2691.

Carlo, T.A., Tewksbury, J.J. & Martinez del Rio, C. (2009) A new method to track seed dispersal and recruitment using ^{15}N isotope enrichment. *Ecology*, **90**, 3516–3525.

Clark, J.S. (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist*, **152**, 204–224.

Clark, J.S., Macklin, E. & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs*, **68**, 213–235.

Clavero, M. & García-Berthou, E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, **20**, 110.

Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (eds) (2001) *Dispersal*. Oxford University Press, Oxford.

Colautti, R.I. & MacIsaac, H.J. (2004) A neutral terminology to define 'invasive' species. *Diversity and Distributions*, **10**, 135–141.

Cousens, R., Dytham, C. & Law, R. (2008) *Dispersal in Plants: A Population Perspective*. Oxford University Press, New York.

Damschen, E.I., Brudvig, L.A., Haddad, N.M., Levey, D.J., Orrock, J.L. & Tewksbury, J.J. (2008) The movement ecology and dynamics of plant communities in fragmented landscapes. *Proceedings of the National Academy of Sciences of the USA*, **105**, 19078–19083.

Debussche, M. & Isenmann, P. (1990) Introduced and cultivated fleshy-fruited plants: consequences for a mutualistic Mediterranean plant-bird system. *Biological Invasions in Europe and the Mediterranean Basin* (ed. F. Di Castri, A.J. Hansen & M. Debussche), pp. 399–416. Kluwer Academic Publishers, Dordrecht.

Dennis, A.J. & Westcott, D.A. (2007) Estimating dispersal kernels produced by a diverse community of vertebrates. *Seed Dispersal: Theory and its Application in a Changing World* (ed. A.J. Dennis, R.J. Green, E.W. Schupp & D.A. Westcott), pp. 201–228. CAB International, Wallingford, UK.

Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M. & Gemmell, N.J. (2005) Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution*, **20**, 470–474.

Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.

Foxcroft, L.C., Rouget, M., Richardson, D.M. & MacFadyen, S. (2004) Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park, South Africa: environmental determinants and propagule pressure. *Diversity and Distributions*, **10**, 427–437.

Godoy, J.A. & Jordano, P. (2001) Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Molecular Ecology*, **10**, 2275–2283.

González-Martínez, S.C., Burczyk, J., Nathan, R., Nanos, N., Gil, L. & Alía, R. (2006) Effective gene dispersal and female reproductive success in Mediterranean maritime pine (*Pinus pinaster* Aiton). *Molecular Ecology*, **15**, 4577–4588.

Hardesty, B.D., Hubbell, S.P. & Bermingham, E. (2006) Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecology Letters*, **9**, 516–525.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.

Hastings, A., Cuddington, K., Davies, K.F., et al. (2005) The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters*, **8**, 91–101.

Hedenström, A., Johansson, L.C. & Spedding, G.R. (2009) Bird or bat: comparing airframe design and flight performance. *Bioinspiration & Biomimetics*, **4**, 015001, doi:10.1088/1748-3182/4/1/015001.

Herrera, C.M. (2002) Seed dispersal by vertebrates. *Plant–Animal Interactions: An Evolutionary Approach* (ed. C.M. Herrera & O. Pellmyr), pp. 185–208. Blackwell, Oxford.

Higgins, S.I. & Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist*, **153**, 464–475.

Higgins, S.I., Clark, J.S., Nathan, R., et al. (2003a) Forecasting plant migration rates: managing uncertainty for risk assessment. *Journal of Ecology*, **91**, 341–347.

Higgins, S.I., Nathan, R. & Cain, M.L. (2003b) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology*, **84**, 1945–1956.

Holbrook, K.M. & Smith, T.B. (2000) Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia*, **125**, 249–257.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–228.

Hulme, P.E., Bacher, S., Kenis, M., et al. (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology*, **45**, 403–414.

Izhaki, I., Korine, C. & Arad, Z. (1995) The effect of bat (*Rousettus aegyptiacus*) dispersal on seed-germination in eastern Mediterranean habitats. *Oecologia*, **101**, 335–342.

Jones, A.G. & Ardren, W.R. (2003) Methods of parentage analysis in natural populations. *Molecular Ecology*, **12**, 2511–2523.

Jones, F.A., Chen, J., Weng, G.J. & Hubbell, S.P. (2005) A genetic evaluation of seed dispersal in the Neotropical tree *Jacaranda copaia* (Bignoniaceae). *American Naturalist*, **166**, 543–555.

Jongejans, E., Shea, K., Skarpaas, O., Kelly, D., Sheppard, A.W. & Woodburn, T.L. (2008) Dispersal and demography contributions to population spread of *Carduus nutans* in its native and invaded ranges. *Journal of Ecology*, **96**, 687–697.

Jordano, P. (2000) Fruits and frugivory. *Seeds: The Ecology of Regeneration in Plant Communities* (ed. M. Fenner), pp. 125–165. CAB International, Wallingford, UK.

Jordano, P., García, C., Godoy, J.A. & García-Castaño, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the USA*, **104**, 3278–3282.

Julliot, C. (1996) Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *International Journal of Primatology*, **17**, 239–258.

Klein, E.K., Lavigne, C. & Gouyon, P.-H. (2006) Mixing of propagules from discrete sources at long distance: comparing a dispersal tail to an exponential. *BMC Ecology*, **6**, 3.

Korine, C., Izhaki, I. & Arad, Z. (1999) Is the Egyptian fruit-bat *Rousettus aegyptiacus* a pest in Israel? An analysis of the bat's diet and implications for its conservation. *Biological Conservation*, **88**, 301–306.

Kot, M., Lewis, M.A. & van den Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77**, 2027–2042.

Kuparinen, A. (2006) Mechanistic models for wind dispersal. *Trends in Plant Science*, **11**, 296–301.

Kwiecinski, G.G. & Griffiths, T.A. (1999) *Rousettus egyptiacus. Mammalian Species*, **611**, 1–9.

Lemke, A., von der Lippe, M. & Kowarik, I. (2009) New opportunities for an old method: using fluorescent colours to measure seed dispersal. *Journal of Applied Ecology*, **46**, 1122–1128.

Levey, D.J. & Sargent, S. (2000) A simple method for tracking vertebrate-dispersed seeds. *Ecology*, **81**, 267–274.

Levey, D.J., Tewksbury, J.J. & Bolker, B.M. (2008) Modelling long-distance seed dispersal in heterogeneous landscapes. *Journal of Ecology*, **96**, 599–608.

Levin, S.A., Muller-Landau, H.C., Nathan, R. & Chave, J. (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology Evolution and Systematics*, **34**, 575–604.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London B*, **270**, 775–781.

Mack, A.L. (1995) Distance and nonrandomness of seed dispersal by the dwarf cassowary *Casuarius bennetti. Ecography*, **18**, 286–295.

Mack, A.L. & Druliner, G. (2003) A non-intrusive method for measuring movements and seed dispersal in cassowaries. *Journal of Field Ornithology*, **74**, 193–196.

Mack, R.N. & Lonsdale, W.M. (2001) Humans as global plant dispersers: getting more than we bargained for. *Bioscience*, **51**, 95–102.

Marshall, A.G. (1983) Bats, flowers and fruit: evolutionary relationships in the Old World. *Biological Journal of the Linnean Society*, **20**, 115–135.

Meagher, T.R. & Thompson, E. (1987) Analysis of parentage for naturally established seedlings of *Chamaelirium luteum* (Liliaceae). *Ecology*, **68**, 803–812.

Mickleburgh, S.P., Hutson, A.M. & Racey, P.A. (1992) *Old World Fruit Bats: An Action Plan For Their Conservation*. International Union for the Conservation of Nature and Natural Resources (IUCN), Gland.

Murphy, H.T., Hardesty, B.D., Fletcher, C.S., Metcalfe, D.J., Westcott, D.A. & Brooks, S.J. (2008) Predicting dispersal and recruitment of *Miconia calvescens* (Melastomaceae) in Australian tropical rainforests. *Biological Invasions*, **10**, 925–936.

Murray, K.G. (1988) Avian seed dispersal of 3 Neotropical gap-dependent plants. *Ecological Monographs*, **58**, 271–298.

Muscarella, R. & Fleming, T.H. (2007) The role of frugivorous bats in tropical forest succession. *Biological Reviews*, **82**, 573–590.

Nakamoto, A., Kinjo, K. & Izawa, M. (2009) The role of Orii's flying-fox (*Pteropus dasymallus inopinatus*) as a pollinator and a seed disperser on Okinawa-jima Island, the Ryukyu Archipelago, Japan. *Ecological Research*, **24**, 405–414.

Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786–788.

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, **15**, 278–285.

Nathan, R., Katul, G.G., Horn, H.S., et al. (2002) Mechanisms of long-distance dispersal of seeds by wind. *Nature*, **418**, 409–413.

Nathan, R., Getz, W.M., Revilla, E., et al. (2008a) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the USA*, **105**, 19052–19059.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008b) Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, **23**, 638–647.

Nathan, R., Bullock, J.M., Ronce, O. & Schurr, F.M. (2009) *Seed dispersal. Encyclopedia of Life Sciences*. John Wiley, Chichester, UK.

Neubert, M.G. & Caswell, H. (2000) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, **81**, 1613–1628.

Okubo, A. & Levin, S.A. (1989) A theoretical framework for data-analysis of wind dispersal of seeds and pollen. *Ecology*, **70**, 329–338.

Ouborg, N.J., Piquot, Y. & van Groenendael, J.M. (1999) Population genetics, molecular markers and the study of dispersal in plants. *Journal of Ecology*, **87**, 551–568.

Pennycuick, C.J. (2008) *Modelling the Flying Bird*. Academic Press, London.

Peterson, A.T. & Vieglais, D.A. (2001) Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *Bioscience*, **51**, 363–371.

Pimentel, D., McNair, S., Janecka, J., et al. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture Ecosystems & Environment*, **84**, 1–20.

Pons, J. & Pausas, J.G. (2007) Acorn dispersal estimated by radio-tracking. *Oecologia*, **153**, 903–911.

Por, F.D. (1978) *Lessepsian Migration*. Springer-Verlag, Berlin.

Reichard, S.H. & White, P. (2001) Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience*, **51**, 103–113.

Ricciardi, A. (2007) Are modern biological invasions an unprecedented form of global change? *Conservation Biology*, **21**, 329–336.

Richardson, D.M. & Pyšek, P. (2008) Fifty years of invasion ecology – the legacy of Charles Elton. *Diversity and Distributions*, **14**, 161–168.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M. (2000a) Plant invasions – the role of mutualisms. *Biological Reviews*, **75**, 65–93.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000b) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.

Robbins, C.T. (1993) *Wildlife Feeding and Nutrition*, 2nd edn. Academic Press, San Diego.

Robledo-Arnuncio, J.J. & García, C. (2007) Estimation of the seed dispersal kernel from exact identification of source plants. *Molecular Ecology*, **16**, 5098–5109.

Rowell, T.E. & Mitchell, B.J. (1991) Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. *Journal of Tropical Ecology*, **7**, 269–274.

Russo, S.E., Portnoy, S. & Augspurger, C.K. (2006) Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology*, **87**, 3160–3174.

Schurr, F.M., Steinitz, O. & Nathan, R. (2008) Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology*, **96**, 628–641.

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A. & Nathan, R. (2009) Long-distance seed dispersal. In *Fruit Development and Seed Dispersal* (ed. L. Østergaard), pp. 204–237. Blackwell, Oxford.

Shilton, L.A., Altringham, J.D., Compton, S.G. & Whittaker, R.J. (1999) Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society of London B*, **266**, 219–223.

Skarpaas, O. & Shea, K. (2007) Dispersal patterns, dispersal mechanisms, and invasion wave speeds for invasive thistles. *American Naturalist*, **170**, 421–430.

Smith, R.M., Thompson, K., Hodgson, J.G., Warren, P.H. & Gaston, K.J. (2006) Urban domestic gardens (IX): Composition and richness of the vascular plant flora, and implications for native biodiversity. *Biological Conservation*, **129**, 312–322.

Soons, M.B. & Bullock, J.M. (2008) Non-random seed abscission, long–distance wind dispersal and plant migration rates. *Journal of Ecology*, **96**, 581–590.

Soons, M.B., Heil, G.W., Nathan, R. & Katul, G.G. (2004) Determinants of long-distance seed dispersal by wind in grasslands. *Ecology*, **85**, 3056–3068.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.

Stevenson, P.R. (2000) Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: dispersal distance, germination rates, and dispersal quantity. *American Journal of Primatology*, **50**, 275–289.

Sun, C. & Moermond, T.C. (1997) Foraging ecology of three sympatric turacos in a montane forest in Rwanda. *Auk*, **114**, 396–404.

Sun, C., Ives, A.R., Kraeuter, H.J. & Moermond, T.C. (1997) Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia*, **112**, 94–103.

Tackenberg, O. (2003) Modeling long-distance dispersal of plant diaspores by wind. *Ecological Monographs*, **73**, 173–189.

Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution*, **21**, 208–216.

Vellend, M., Myers, J.A., Gardescu, S. & Marks, P.L. (2003) Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology*, **84**, 1067–1072.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.

Von der Lippe, M. & Kowarik, I. (2007) Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conservation Biology*, **21**, 986–996.

Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology & Evolution*, **17**, 379–385.

Ward, M.J. & Paton, D.C. (2007) Predicting mistletoe seed shadow and patterns of seed rain from movements of the mistletoebird, *Dicaeum hirundinaceum*. *Austral Ecology*, **32**, 113–121.

Wehncke, E.V., Hubbell, S.P., Foster, R.B. & Dalling, J.W. (2003) Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species. *Journal of Ecology*, **91**, 677–685.

Weir, J.E.S. & Corlett, R.T. (2007) How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landscape Ecology*, **22**, 131–140.

Westcott, D.A. & Graham, D.L. (2000) Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia*, **122**, 249–257.

Westcott, D.A., Bentrupperbäumer, J., Bradford, M.G. & McKeown, A. (2005) Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, **146**, 57–67.

Westcott, D.A., Setter, M., Bradford, M.G., McKeown, A. & Setter, S. (2008) Cassowary dispersal of the invasive pond apple in a tropical rainforest: the contribution of subordinate dispersal modes in invasion. *Diversity and Distributions*, **14**, 432–439.

Wheelwright, N.T. & Orians, G.H. (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist*, **119**, 402–413.

With, K.A. (2002) The landscape ecology of invasive spread. *Conservation Biology*, **16**, 1192–1203.

Wright, S.J., Trakhtenbrot, A., Bohrer, G., et al. (2008) Understanding strategies for seed dispersal by wind under contrasting atmospheric conditions. *Proceedings of the National Academy of Sciences of the USA*, **105**, 19084–19089.

Xiao, Z.S., Jansen, P.A. & Zhang, Z.B. (2006) Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *Forest Ecology and Management*, **223**, 18–23.

Zhang, S.Y. & Wang, L.X. (1995) Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. *Biotropica*, **27**, 397–401.

4. GENERAL DISCUSSION AND CONCLUSIONS

Summary and integration of results

This dissertation explores various aspects of the movement ecology of a flying frugivore, the Egyptian fruit bat (*Rousettus aegyptiacus*). To summarize and discuss the results, I will deal first with the daily foraging flight pattern and how it is affected by the distribution of food resources (fruit trees). I will then examine the capacity and mechanism of the bats' long distance navigation, and then tackle the potential role of bats as long-distance dispersers of plant seeds and of invasive plant species in particular. For each of these subjects, the underlying processes and their consequences will be discussed, addressing the objectives set forth in the Introduction (section 1.6). I will then integrate the results by employing the movement ecology framework. In the next section (section 4.2), methodological issues, practical implications, and directions for future research will be addressed.

Bats' daily foraging movements:

Bats fly from the roost to a selected fruit tree by means of long, high and straight commuting flights (figure 2). Long distance foraging flights has been shown previously in fruit bats (Morrison 1978a; Fleming 1988; Andrianaivoarivelo *et al.* 2008), although not with the great precision carried out in the present research. The bats' flight altitude was found to be much higher than that of any of the surrounding landscape features of the terrain (mean of 103.8 m above ground level; table 1) that might be explained by predation avoidance (flying above the flight altitude of owls) or the need for visual navigational cues, as reported in this thesis (Tsoar *et al.* 2011a). Recently there have been indirect observations of fruit bats flying at such high altitudes (Parsons *et al.* 2008). The bat's direct flight and its repeated flights to the foraging site, indicates its intention to fly to that site before it started its flight. Interestingly, its commuting flight speed is much below that expected from theoretical modeling (Norberg & Rayner 1987; Pennycuick 2008). I was surprised to find that the bats commuting flight speed was at the speed of the predicted minimum power speed (V_{mp}) by the Pennycuick (2008) model and not by the maximal range speed (V_{mr}). This can be explained by either the bats considering other factors while optimizing (Grodzinski *et al.* 2009) their flight speed.

Bats showed high tree and route fidelity during consecutive nights (figure 4), Homing experiments showed the degree of fidelity the bats have to their roost and foraging tree, returning to the same specific location for far away distances.

Commuting bats often ignoring nearby fruit trees with the same ripeness of fruit a behavior previously observed in other fruit-bats in different parts of the world (Fleming *et al.* 1977; Heithaus *et al.* 1978; Morrison 1978a; Lemke 1984; Fleming & Heithaus 1986; Tang *et al.* 2010). The bats foraging pattern showed a clear interaction with the resource distribution within the landscape. The next stage was to examine the resource distribution in relation to the bats' foraging movements.

Bats as optimal foragers:

We used the tree distribution map created especially for the present research to study the effect of tree distribution within the landscape with respect to the distribution of the bats. There has been a need for some time for full detailed maps of locations of all consumed species (Matthiopoulos 2003; Nathan *et al.* 2008a; Wakefield *et al.* 2009; Owen-Smith *et al.* 2010; Bridge *et al.* 2011). Most mapping of landscape resources use either habitat type maps or transect sampling that do not map the actual distribution of the resource (Heithaus *et al.* 1978; Fleming & Heithaus 1986; Fleming 1988; Cosson *et al.* 1999; Mcconkey & Drake 2007; Richter & Cumming 2008) or like Morrison (1978b) mapped only a single resource species. The high resolution map constructed for the present research enabled creating a simplified model of the attractiveness (figure 5) of the landscape to the bats by taking into consideration the benefit (tree density) in relation to the cost (distance from the roost). This attractiveness map enabled a better understanding of the spatial distribution of the bats. For example, the bats did not select the closest fruit trees with ripe fruit but preferred to forage further away from the roost (figure 3).Examining the mean attractiveness score of the closest fruit trees to the roost showed them to be as expected by a random selection, while the actual foraging locations the bats selected were on average much higher than would be expected by a random selection of sites. The result showed that bats optimized their energy expenditure by selecting fruit trees that were relatively close to the roost, and by selecting attractive locations in terms of food abundance versus travel distance. Although bat movement has been studied, little is known about the mechanisms of their navigation at long distances (Holland 2007).

Bat navigation:

The work on the second chapter was in fact motivated by the principal finding of the first chapter—that bats fly in such a directed long flight to a specific target, triggered the need to explore their navigation capacity. In this second chapter, the bats were shown to be well familiar with their surroundings and capable of long distance navigation over unfamiliar territory while showing a remarkable ability to home back to their roost or familiar fruit tree over distances of up to 100 km—returned in a very straight and direct flight back to their familiar area. It is clearly demonstrated that bats use visual cues for long range navigation, along with other cues. This emerged due to the fact that all in-crater released bats left the crater in a general northerly direction, indicating that the bats possess a cognitive map of their surroundings (O’Keefe & Nadel 1978) but still use visual cues to assist in their long distance navigation. It has been suggested that microbats use the earth's magnetic field for long range navigation (Holland *et al.* 2006, 2008; Holland, Borissov, & Siemers 2010; Tian *et al.* 2010), it is yet to be discovered whether fruit bats have a similar mechanism. Moreover, the fact that the bats do not relay on a single input for their orientation is not surprising as other organisms also show a multiple sensory input for orientation (Baldaccini *et al.* 1976; Lipp *et al.* 2004; Wallraff 2005).

Bats as dispersers of invasive plant species:

The third chapter of this dissertation also has its roots in the findings of the first chapter. The long distance flights of the bats imply they can make an important contribution to the seed dispersal of the plants on which they feed (Marshall 1983; Fujita

& Tuttle 1991; Muscarella & Fleming 2007; Jones *et al.* 2009). Modeling the potential seed dispersal (Sun *et al.* 1997; Loiselle & Blake 1999; Holbrook & Smith 2000), established that the bats flew long distances to restricted foraging sites, generated complex seed shadows (dispersing seeds to distances of up to 20 km) with peaks at the vicinity of fruiting and non fruiting trees. It was also found that the dispersal distance kernel is strongly affected by the spatial distribution of the fruiting trees, rather 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 speeds and gut retention times are relatively similar.

Thus, due to their long and fast flight, the bats are important seed dispersers, dispersing seeds to very long distances.

A recent work found the Tambaqui fish (Anderson *et al.* 2011) to be an extremely long distance seed disperser mainly due to its long gut retention time and relative long movements during annual floods. The present research showed the Egyptian fruit bat to potentially disperse seeds to mean and maximum distances of 1,215 m and 20,671 m respectively. These are much longer than the predicted 337 m and 5,495 m found by Anderson et al. (2011). In contrast to his findings, no difference was found in the gut retention time between different plant species that were consumed by the bat.

To date, the Egyptian fruit bat shows one of the longest mean dispersal distances, coming after the Black-casqued Hornbill (1,521 m), White-thighed Hornbill (1,537 m), (Holbrook & Smith 2000) and the Asian Elephant (1,988 m) (Campos-Arceiz *et al.* 2008). To my knowledge, the maximum dispersal distance estimated in this study is the longest documented to date (20,671 m). When comparing between the studies, it seems that the bats longer dispersal distance is mainly due to its foraging pattern of long fast commuting flights, enabling the bat to disperse seeds to long distances even when its gut retention time is relatively short. The Egyptian fruit bat is exceptional among mammals in its mean seed dispersal distance, even when compared with flying frugivorous birds.

Some of the traits also make the Egyptian fruit bat a potential hazard for distributing invasive plants, traits such as: its generalist feeding habit, preference for foraging near settlements and its long return flight to the roost, which is often over natural habitats. We have shown such traits in the Egyptian fruit bat but these are probably common in fruit bats (Muscarella & Fleming 2007).

Movement ecology – the unifying framework:

The movement ecology paradigm enabled working within a comprehensible framework and relating different aspects of the animal's movement. It has especially helped in articulating the complicated animal-seed relations of endozoochory, as explained in detail in chapter three of this work.

By using the movement ecology framework I have been able to put these three chapters in a unifying template of the movement of bats. As mentioned in the introduction (section 1.1) this framework asserts that four basic components are needed to describe any type of movement by any organisms: (1) the internal state from which the individual’s motivation to move is derived; two constraints – (2) the navigation capacity, and (3) the motion capacity of the individual organism that reflect, respectively, the mechanisms used to execute movement and to decide where and when to move; and (4) the broad set of biotic and abiotic external factors affecting each of the three components above.

In chapter one, I focused on the foraging movement to and from the fruit tree (internal state and motion capacity) in relation to the distribution of food resources (external factors and navigation capacity) within the landscape. In chapter two, I focused on how bats return home (internal state) after translocation to remote sites (navigation capacity and external factors) and the underlying mechanism for that. In chapter three, I employ a nested design of the movement ecology framework, in which the movement ecology of the plants is nested within the movement ecology of the bats. Here, the bats are the key external factor for the movement of the seeds, and the trees and fruits are the main external factors determining the movement of the bats.

The common theme of all three chapters in this thesis is the movement ecology of the Egyptian fruit bat, describing its movement pattern and navigation ability, the factors affecting it and how all these factors are expected to impact other organisms.

Methodological issues, practical implications and directions for future research:

This thesis introduces four novel methodologies developed for this research.

This was the first time GPS technology was used in tracking bat movements; the ultra high resolution capacity enabled determination of complete (full) night movement of bats in high accuracy in time and place. Such a detailed tracking methodology has never previously been carried out in the wild and at such a large spatial scale. Although the high sampling rate reduced the tracking duration per bat, that was compensated by supplementing data collection by manually tracking with radio telemetry and by a relatively large sample size of the marked GPS bats (in total 74). The high resolution detailed tracking enabled extracting accurate information regarding the exact foraging location, flight routes, as well as flight parameters, for each of the tracked bats.

The second novel methodology employed was the creation and use of an attractiveness map for testing optimal foraging by testing the site location selected by the bats compared to other possible options. Such a map was enabled due to the high resolution movement of the bats, and the high resolution mapping of fruit trees within a large scale of the familiar area of the bats. The attractiveness map seems to better explain previous observations on the foraging behavior of some of the fruit bats worldwide(Fleming *et al.* 1977; Heithaus *et al.* 1978; Morrison 1978b; Fleming & Heithaus 1986). Its strength is in its simplicity, although sensitivity analysis is still needed for testing the model's robustness and for extracting case specific parameters.

The third novel methodology was the design of the homing experiments, of a large-scale geological formation, a natural erosional crater ("HaMakhtesh HaGadol"), to manipulate the visual cues of the homing bat. I also manipulated the goal location by two treatments, hungry bats aim to fly to their foraging sites while well-fed bats released towards the end of the night aim their return flight to their roost. This is the first time such navigational abilities have been demonstrated in a mammal. The present finding received some attention within the scientific community due to its originality and the important implications to additional fields of research such as neuroscience (Moser 2011).

The fourth novel methodology was the development of an allometric function to define the potential distance of a vector to disperse seeds by endozoochory.-The allometric model developed in this research has great potential for use as a kind of a null model for the probability of seed dispersal within a given community of species. This model enables to (a) predicting within an ecological community the seed dispersal of each vector and calculating the overall potential distribution of distances of the dispersed seeds (Nathan *et al.* 2008b). That, in turn, enables to evaluate the potential seed dispersal within an entire ecological community and is expected to be an important tool for meta-community analysis. In addition, the model can be used to (b) compare any quantitative result of a vector with a "null model" of that vector's potential to disperse seeds. The use of the model in the present research showed that bats are a kind of a "super” LDD vector.

Analyzing the movement ecology of the Egyptian fruit bat is an important contribution to wildlife management. Until recently in Israel, under the pretence that the bat caused damage to agriculture, it was common practice to eradicate fruit bats by fumigating the bats’ roost (Makin 1990; Korine, Izhaki, & Arad 1999). Causing the unnecessary death of all organisms within the fumigated cave (Makin & Mendelssohn 1987). The present research showed that bats feed from specific pre-selected fruit trees and stay loyal to those trees for some time. Moreover, that the foraging bats do not necessarily come from the closest roost to feed from that specific tree. The bats’ long commuting flight, as found in this research, makes the roost location almost irrelevant in regards to the origin of the bats causing the agricultural damage. Thus, we may conclude that fumigation of the entire roost is impractical, as fruit bats do not necessarily fly to the orchard from the closest roost. Because bats show high fidelity to specific fruit trees and may be visiting a specific orchard from a distant roost, the recommended practice should be to capture the particular bats coming to the damaged orchard.

To correctly eradicate fruit bats from an orchard, the following steps should be employed:

a) Carrying out a survey of the alleged damaged orchard by a bat specialist to ensure the damage is indeed caused by fruit bats, and to evaluate the damaged caused.

b) If possible, covering the fruit trees with nets to prevent the fruit bats access to the fruit. Also, it is recommended to surround the orchard with small moving obstacles, such as old CD disks, and motion-activated lighting, that might repel the bats.

c) If the previous suggestions do not solve the immediate problem, then deploying mist nets to capture the visiting fruit bats, and removing them from the area. Bats may return even if released far away, as shown in chapter 2. Thus, it might be necessary to hold the captured bats in captivity until the fruit is picked and only then release them back to the wild.

It is important to emphasis that roost fumigation had, in the past, severe ecological implications for Israeli cave fauna and is presently considered to be one of the major causes for the reduction and extinction of some of the insectivorous bat populations in Israel.

I have shown that the Egyptian fruit bat can be a long distance dispersal vector of seeds, this emphasizes its importance for the well being of the natural habitat especially in a crowded country such as Israel. But such a seed dispersal service does not come for free as the bat has been shown to potentially disperse invasive species as well. Due to these findings I suggest to begin a monitoring program of dropped seeds by bats.

The best method might be to monitor the floor of a bat roost to examine if seeds that originate from invasive species have been dropped to the roost floor by the resting bats.

This research has shown that the Egyptian fruit bat is an exceptional model for studying animal navigation due to its relatively high motivation to return to its original roost and its ability to do so from relatively long distances, a motivation similar and some times even stronger than that of homing pigeons.

We have found the bats to fly long distances to specific trees (3.1), presumably guided by distal visual cues (3.2). The finding that they favor attractive sites (3.1) implies they are well familiar with the variation in resource attractiveness in the landscape. The bats may collect the information on their own or by information transfer between individuals within the colony or at the feeding sites. Interesting research question will be to monitor the bat activity at these meeting places (roost to foraging tree) that are most likely information transfer sites.

We are presently entering a new technological era of miniaturized GPS devices enabling recording of high quality data at a high tempo-spatial resolution. With this technological advance, there is a need for new tools for data analysis. For example, one of the current limitations is the GPS not being able to accurately record locations when the GPS is not moving or moving very slowly. That limits our ability to differentiate between a non moving/resting behavior and a limited moving feeding behavior within the tree. In future, creation of new statistical and mathematical tools is needed to enable differentiating between these behaviors.

Another methodological issue is the lack of ability to carry out remote downloading of data from the GPS. Our GPS model did not have simple and energetically cheap download possibilities, A limitation that has recently been solved. In this work we had to physically hold the GPS device in order to retrieve the data. If a GPS device was not recovered, we could not obtain the data, even if the telemetry device attached to the GPS could be heard in the roost. This caused loss of data in some cases, because although the bat was heard in the roost, but the GPS could not be found. This issue will be solved once battery efficiency will be sufficient to support such an energy-consuming apparatus.

Thanks to the new technological innovation of the miniaturized GPS devices, there are unlimited research questions that can be tested. For example, one of the most interesting topics aspects of animal movement is the social aspect while foraging, and how does the social aspect affect the individuals navigational ability (Simons 2004; Dell'Ariccia *et al.* 2008) Our findings raise new questions regarding the bats navigational and foraging ability, for example, do they use group navigation? Does information pass between individuals about newly found resources? Do the bats forage by predefined subgroups and, if so, are they genetically related? What are the additional environmental cues used by the bats for their orientation and long-range navigation? How does the social structure and rank affect their movement pattern? Do the bats show the "many-wrongs" principle?

The present thesis has opened new horizons for bat research showing the huge advantage there is in the use of GPS technology for the study of the different aspects of bat's movement ecology. Newer and better GPS models are constantly being developed and undoubtedly newer and better models will be available to ecologists for the research of medium and small animals in general and for bat research in particular. Yet, it is important to remember that whereas good technology is not a substitute for good science (Hebblewhite & Haydon 2010), good theory is a crucial part of good science.

5. REFERENCES

Abdi, H. (2007) The Bonferonni and Šidák Corrections for Multiple Comparisons. In: Salkind, N., (ed.). *Encyclopedia of Measurement and Statistics.* Sage Publication, Thousand Oaks

Aldridge, H.D.J.N. & Brigham, R.M. (1988) Load Carrying and Maneuverability in an Insectivorous Bat: A Test of the 5% “Rule” of Radio -Telemetry. *Journal of Mammalogy*, **69**, 379-382.

Anderson, J.T., Nuttle, T., Saldaña Rojas, J.S., Pendergast, T.H. & Flecker, A.S. (2011) Extremely long-distance seed dispersal by an overfished Amazonian frugivore. *Proceedings of the Royal Society of London Series B*, **278**, 3329-3335.

Andrianaivoarivelo, R. A., Ramilijaona, O.R., Racey, P.A., Razafindrakoto, N. & Jenkins, R.K.B. (2011) Feeding ecology, habitat use and reproduction of *Rousettus madagascariensis* Grandidier, 1928 (Chiroptera: Pteropodidae) in eastern Madagascar. *Mammalia*, **75**, 69-78.

Andrianaivoarivelo, A.R., Shore, G.D., McGuire, S.M., Jenkins, R.K.B., Ramilijaona, O., Louis, E.E. & Brenneman, R.A. (2008) Characterization of 22 microsatellite marker loci in the Madagascar rousette (*Rousettus madagascariensis*). *Conservation Genetics*, **10**, 1025-1028.

Baker, R.R. (1978) *The Evolutionary Ecology of Animal Migration*. Hodder and Stoughton.

Baldaccini, N.E., Benvenuti, S. & Fiaschi, V. (1976) Homing Behavior of Pigeons Confined to a New Loft Distant from their Home. *Monitore Zoologico Italiano-Italian Journal of Zoology*, **10**, 461-467.

Barclay, R.M.R. & Jacobs, D.S. (2011) Differences in the foraging behaviour of male and female Egyptian fruit bats (*Rousettus aegyptiacus*). *Canadian Journal of Zoology*, **89**, 466-473.

Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M. & Melian, C.J. (2003) The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 9383-9387.

Bennett, A.T.D. (1996) Do animals have cognitive maps? *Journal of Experimental Biology*, **199**, 219-224.

Bingman, V.P. & Cheng, K. (2005) Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethology Ecology & Evolution*, **17**, 295-318.

Biro, D., Guilford, T., Dell'Omo, G. & Lipp, H.-P. (2002) How the viewing of familiar landscapes prior to release allows pigeons to home faster: evidence from GPS tracking. *The Journal of Experimental Biology*, **205**, 3833-3844.

Boles, L.C. & Lohmann, K.J. (2003) True navigation and magnetic maps in spiny lobsters. *Nature*, **421**, 60-63.

Bolmgren, K. & Eriksson, O. (2005) Fleshy fruits - origins, niche shifts, and diversification. *Oikos*, **109**, 255-272

Bovet, P. & Benhamou, S. (1991) Optimal Sinuosity in Central Place Foraging Movements. *Animal Behaviour*, **42**, 57-62.

Bowlin, M.S., Bisson, I.A., Shamoun-Baranes, J., Reichard, J.D., Sapir, N., Marra, P.P., Kunz, T.H., Wilcove, D.S., Hedenstrom, A., Guglielmo, C.G., Akesson, S., Ramenofsky, M. & Wikelski, M. (2010) Integrating concepts and technologies to advance the study of bird migration. *Integrative and Comparative Biology*, **50**, 261-279.

Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Kays, R., Kelly, J.F., Robinson, W.D. & Wikelski, M. (2011) Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. *BioScience*, **61**, 689-698.

Buckley, Y.M., Anderson, S., Catterall, C.P., Corlett, R.T., Engel, T., Gosper, C.R., Nathan, R., Richardson, D.M., Setter, M., Spiegel, O., Vivian-Smith, G., Voigt, F.A., Weir, J.E.S. & Westcott, D.A. (2006) Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology*, **43**, 848-857.

Bullock, J.M., Kenward, K.E. & Hails, R.S. (2002) *Dispersal ecology.* Cambridge University Press, Cambridge.

Calder, W.A. (1984) *Size, Function and Life History,* (2nd ed). Dover Publications, Cambridge.

Campos-Arceiz, A., Larrinaga, A.R., Weerasinghe, U.R., Takatsuki, S., Pastorini, J., Leimgruber, P., Fernando, P. & Santamaría, L. (2008) Behavior rather than diet mediates seasonal differences in seed dispersal by Asian elephants. *Ecology*, **89**, 2684-2691.

Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (2001) *Dispersal*. Oxford University Press, Oxford.

Cochran, W.W., Mouritsen, H. & Wikelski, M. (2004) Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science*, **304**, 405-408.

Cosson, J.F., Pons, J.M. & Masson, D. (1999) Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *Journal of Tropical Ecology*, **15**, 515-534.

Dell'Ariccia, G., Dell'Omo, G., Wolfer, D.P. & Lipp, H.P. (2008) Flock flying improves pigeons' homing: GPS track analysis of individual flyers versus small groups. *Animal Behavior*, **76**, 1165-1172.

Dingle, H. (1996) *Migration: the biology of life on the move*. Oxford University Press, Oxford.

Fenton, M.B., Rautenbach, I.L., Smith, S.E., Swanepoel, C.M., Grosell, J. & Vanjaarsveld, J. (1994) Raptors and Bats - Threats and Opportunities. *Animal Behaviour*, **48**, 9-18.

Fleming, T.H. (1988) *The Short-tailed Fruit Bat: A Study in Plant-Animal Interactions*. (2nd ed). University of Chicago Press, Chicago.

Fleming, T.H. & Heithaus, E.R. (1981) Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica*, **13**, 45-53.

Fleming, T.H. & Heithaus, E.R. (1986) Seasonal Foraging Behavior of the Frugivorous Bat Carollia-Perspicillata. *Journal of Mammalogy*, **67**, 660-671.

Fleming, T.H., Heithaus, E.R. & Sawyer, W.B. (1977) Experimental-Analysis of Food Location Behavior of Frugivorous Bats. *Ecology*, **58**, 619-627.

Fretwell, S.D. (1972) Populations in a seasonal environment. *Monographs in Population Biology*,**5**, 1-217.

Fretwell, S.D. & Lucas Jr., H.L. (1969) On territorial behavioral and other factors influencing habitat distribution in birds: I. Theoretical development. *Acta Biotheoretica*, **19**, 16-36.

Fujita, M.S. & Tuttle, M.D. (1991) Flying foxes (Chiroptera, Pteropodidae) - Threatened animals of key ecological and economic importance. *Conservation Biology*, **5**, 455-463.

Gallistel, C.R. (1990) *The Organization of Learning*. MIT Press, Cambridge.

Greenberg, R.S. & Marra, P.P. (2005) *Birds of Two worlds: The Ecology and Evolution of Migration*. The John Hopkins University Press, Baltimore.

Griffin, D.R. (1964) *Bird Migration*. Double day, Garden City.

Grodzinski, U., Spiegel, O., Korine, C. & Holderied, M.W. (2009) Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*? *The Journal of Animal Ecology*, **78**, 540-8.

Hebblewhite, M. & Haydon, D.T. (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**, 2303-2312.

Heithaus, E.R., Fleming, T.H. & Opler, P.A. (1975) Foraging Patterns and Resource Utilization in Seven Species of Bats in a Seasonal Tropical Forest. *Ecology*, **56**, 841-854.

Heithaus, E.R., Fleming, T.H., Monographs, E. & Spring, N. (1978) Foraging Movements of a Frugivorous Bat , *Carollia perspicillata* (Phyllostomatidae). *Ecological Monographs*, **48**, 127-143.

Henry, M., Pons, J-M., M. & Cosson, J-F.,F. (2007) Foraging behaviour of a frugivorous bat helps bridge landscape connectivity and ecological processes in a fragmented rainforest. *Journal of Animal Ecology*, **76**, 801-813.

Herrera, C.M. (1985) Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos*, **44**, 132-141.

Hodgkison, R., Balding, S.T. & Kunz, T.H. (2003) Fruit Bats

(Chiroptera: Pteropodidae) as Seed Dispersers and Pollinators in a Lowland Malaysian Rain Forest. *Biotropica*, **35**, 491-502.

Holbrook, K.M. & Smith, T.B. (2000) Seed dispersal and movement patterns in two species of Ceratogymna hornbills in a West African tropical lowland forest. *Oecologia*, **125**, 249-257.

Holland, R.A. (2007) Orientation and navigation in bats: known unknowns or unknown unknowns? *Behavioral Ecology and Sociobiology*, **61**, 653-660.

Holland, R.A., Borissov, I. & Siemers, B.M. (2010) A nocturnal mammal, the greater mouse-eared bat, calibrates a magnetic compass by the sun. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 6941-6945.

Holland, R.A, Kirschvink, J.L., Doak, T.G. & Wikelski, M. (2008) Bats use magnetite to detect the earth’s magnetic field. *PloS ONE*, **3**, e1676.

Holland, R. A, Thorup, K., Vonhof, M.J., Cochran, W.W. & Wikelski, M. (2006) Navigation - bat orientation using earth’s magnetic field. *Nature*, **444**, 702.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. & Spiegel, O. (2008) Trends and missing parts in the study of movement ecology. *Proceedings of the National*

Academy of Sciences of the United States of America, **105**, 19060-19065.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201-228.

Hulme, P.E., Bacher, S., Kenis, M., Klotz, S., Kuhn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., Pyšek, P., Roques, A., Sol, D., Solarz, W. & Vilà, M. (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology*, **45**, 403-414.

Ingle, N.R. (2003) Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. *Oecologia*, **134**, 251-261.

Isard, S.A. & Gage, S.H. (2001) *Flow of Life in the Atmosphere*. Michigan State University Press, East Lansing.

Izhaki, I., Korine, C. & Arad, Z. (1995) The effect of bat (*Rousettus aegyptiacus*) dispersal on seed-germination in eastern Mediterranean habitats. *Oecologia*, **101**, 335-342.

Jacobsen, N.H.G. & Du Plessis, E. (1976) Observations on the ecology and biology of the Cape Fruit bat *Rousettus aegyptiacus leachi* in the eastern Transvaal. *South African Journal of Science*, **72**, 270-273.

Jacobsen, N.H.G., Viljoen, P.C. & Ferguson, W. (1986) Radio tracking of problem fruit bats (*Rousettus aegyptiacus*) in the Transvaal with notes on flight and energetics. *Zeitschrift fur Saugetierkunde-International Journal of Mammalian Biology*, **51**, 205-208.

Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, **8**, 93-115.

Jonsen, I.D., Flenming, J.M. & Myers, R.A. (2005) Robust state-space modeling of animal movement data. *Ecology*, **86**, 2874-2880.

Jonsen, I.D., Myers, R.A. & Flemming, J.M. (2003) Meta-analysis of animal movement using state-space models. *Ecology*, **84**, 3055-3063.

Jordano, P., Garcia, C., Godoy, J.A. & Garcia-Castano, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3278-3282.

Kalko, E.K.V., Herre, E.A. & Handley, C.O. (1996) Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *Journal of Biogeography*, **23**, 565-576.

Kaplan, E.D. & Hegarty, C. (2005) *Understanding GPS: Principles and Applications,* (2nd ed). Artech House Publishers, Norwood.

Katz, M.W., Abramsky, Z., Kotler, B., Altstein, O. & Rosenzweig, M.L. (2010) Playing the waiting game: predator and prey in a test environment. *Evolutionary Ecology Research*, **12,** 793-801.

Kennedy, M. & Gray, R.D. (1993) Can Ecological Theory Predict the Distribution of Foraging Animals - a Critical Analysis of Experiments On the Ideal Free Distribution. *Oikos*, **68**, 158-166.

Korine, C., Izhaki, I. & Arad, Z. (1998) Comparison of fruit syndromes between the Egyptian fruit-bat (*Rousettus aegyptiacus*) and birds in East Mediterranean habitats. *Acta Oecologica*, **19**, 147-153.

Korine, C., Izhaki, I. & Arad, Z. (1999) Is the Egyptian fruit-bat *Rousettus aegyptiacus* a pest in Israel? An analysis of the bat's diet and implications for its conservation. *Biological Conservation*, **88**, 301-306.

Korine, C., Izhaki, I. & Makin, D. (1994) Population-structure and emergence order in the Fruit-bat (*Rousettus aegyptiacus*, Mammalia, Chiroptera). *Journal of Zoology*, **232**, 163-174.

Krivan, V., Cressman, R. & Schneider, C. (2008) The ideal free distribution: A review and synthesis of the game-theoretic perspective. *Theoretical Population Biology*, **73**, 403-425.

Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, **1223**, 1-38.

Kwiecinski, G.G. & Griffiths, T.A. (1999) *Rousettus egyptiacus*. *Mammalian Species*, **611**, 1-9.

Lemke, T.O. (1984) Foraging Ecology of the Long-Nosed Bat, *Glossophaga soricina*, with Respect to Resource Availability. *Ecology*, **65**, 538-548.

Levey, D.J., Silva, W.R. & Galett, M. (2002) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International Press, Wallington.

Levin, S.A., Muller-landau, H.C. & Nathan, R. (2003) The Ecology and Evolution of seed dispersal: A Theoretical Perspective. *Annual Review of Ecology Evolution and Systematics*, **34,** 575-604.

Lewis, S.E. (1995) Roost fidelity of bats - a review. *Journal of Mammalogy*, **76**, 481-496.

Lipp, H.P., Vyssotski, A.L., Wolfer, D.P., Renaudineau, S., Savini, M., Troster, G., & Dell’Omo, G. (2004) Pigeon homing along highways and exits. *Current Biology*, **14**, 1239-1249.

Lohmann, K., Lohmann, C., Ehrhart, L., Bagley, D. & Swing, T. (2004) Animal behaviour - Geomagnetic map used in sea-turtle navigation. *Nature*, **428**, 909-910.

Loiselle, B.A. & Blake, J.G. (1999) Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. *Ecology*, **80**, 330-336.

Makin, D. (1977) *The distribution and biology of insectivorous bats (Microchiroptera) of Israel*. The Hebrew University of Jerusalem, M.Sc. thesis. In Hebrew.

Makin, D. (1990) *Aspects of the Biology of the Fruit Bat Rousettus aegyptiacus in Israel*. Tel-Aviv University. Ph.D. Thesis. In Hebrew.

Makin, D. & Mendelssohn, H. (1985) Insectivorous bats victims of Israeli campaign. *Bats*, **2**, 1-4.

Makin, D. & Mendelssohn, H. (1987) The fruit-bat issue in Israel. *Bats*, **11**, 4-5.

Marshall, A.G. (1983) Bats, flowers and fruit - evolutionary relationships in the old world. *Biological Journal of the Linnean Society*, **20**, 115-135.

Matthiopoulos, J. (2003) The use of space by animals as a function of accessibility and preference. *Ecological Modelling*, **159**, 239-268.

McConkey, K.R. & Drake, D.R. (2007) Indirect Evidence that Flying Foxes Track Food Resources Among Islands in a Pacific Archipelago. *Biotropica*, **39**, 436-440.

McDonald-Madden, E., Schreiber, E.S.G., Forsyth, D.M., Choquenot, D. & Clancy, T.F. (2005) Factors affecting Grey-headed Flying-fox (*Pteropus poliocephalus*: Pteropodidae) foraging in the Melbourne metropolitan area, Australia. *Austral Ecology*, **30**, 600-608.

Mendelssohn, H. & Yom-Tov, Y. (1999) *Fauna Palaestina, Mammalia of Israel*. The Israel Academy of Science and Humanities, Jerusalem.

Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R., Bundrock, G., Hülse, S., Plümpe, T., Schaupp, F., Stach, S., Stindt, J., Stollhoff, N., Watzl, S., Brunke, S., Plu, T. & Schu, E. (2005) Honey bees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Science*, **102**, 3040-3045.

Mickleburgh, S.P., Huston, A.M. & Racey, P.A. (1992) *Old World fruit bats: an action plan for their conservation* .IUCN, Cambridge.

Mills, K.J., Patterson, B.R. & Murray, D.L. (2006) Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. *Wildlife Society Bulletin*, **34**, 1463-1469.

Morris, R.G.M., Garrud, P., Rawlins, J.N.P. & Okeefe, J. (1982) Place Navigation Impaired in Rats with Hippocampal-Lesions. *Nature*, **297**, 681-683.

Morrison, D.W. (1978a) Optimal searching strategy for refuging predators. *American Naturalist*, **112**, 925-934.

Morrison, D.W. (1978b) Influence of Habitat on the Foraging Distances of the Fruit Bat *Artibeus jamaicensis*. *Journal of Mammalogy*, **59**, 622-624.

Moser, E.I. (2011) A bat’s perspective on navigation. *Proceedings of the National*

Academy of Sciences of the United States of America, **108**, 15665-15666.

Murray, K.G. (1988) Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs*, **58**, 271-298.

Muscarella, R. & Fleming, T.H. (2007) The role of frugivorous bats in tropical forest succession. *Biological Reviews*, **82**, 573-590.

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, **15**, 278-285.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008a) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19052-19059.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008b) Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, **23**, 638-647.

Olsson, O., Brown, J.S. & Helf, K.L. (2008) A guide to central place effects in foraging. *Theoretical Population Biology*, **74**, 22-33.

Orians, G.H. & Pearson, N.E. (1979) On the theory of central place foraging. *Analysis of Ecological Systems* (eds D.J. Horn, R.D. Mitchell & G.R. Stairs), pp. 154-177. Ohio State University Press, Columbus.

Owen-Smith, N., Fryxell, J.M. & Merrill, E.H. (2010) Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2267-78.

O'Keefe, J. & Nadel, L. (1978) *The Hippocampus as a Cognitive Map*. Oxford University Press, Oxford.

Parsons, J.G., Blair, D., Luly, J. & Robson, S.K.A. (2008) Flying-fox (Megachiroptera: Pteropodidae) flight altitudes determined via an unusual sampling method: aircraft strikes in Australia. *Acta Chiropterologica*, **10**, 377-379.

Pennycuick, C.J. (2008) *Modelling the Flying Bird*. Academic Press, London.

Perdeck, A.C. (1953) Two types of orientation in migrating starlings, *Sturnus vulgaris* and chaffinches, *Fringilla coelebs*, as revealed by displacement experiments. *Ardea*, **46**, 1-37.

Pierce, G.J. & Ollason, J.G. (1987) Eight reasons why optimal foraging is a complete waste of time. *Oikos*, **49**, 111–118.

van der Pijl, L. (1982) Principles of dispersal in higher plants. Springer-Verlag, Berlin.

Pyke, G.H. (1984) Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics*, **15**, 523-575.

Raghuram, H., Thangadurai, C., Gopukumar, N., Nathar, K. & Sripathi, K. (2009) The role of olfaction and vision in the foraging behaviour of an echolocating megachiropteran fruit bat, *Rousettus leschenaulti* (Pteropodidae). *Mammalian Biology Zeitschrift fur Saugetierkunde*, **74**, 9-14.

Richter, H.V. & Cumming, G.S. (2005) Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *Journal of Zoology*, **268**, 35-44.

Richter, H.V. & Cumming, G.S. (2008) First application of satellite telemetry to track African straw-coloured fruit bat migration. *Journal of Zoology*, **275**, 172-176.

Riskin, D.K., Iriarte-Díaz, J., Middleton, K.M., Breuer, K.S. & Swartz, S.M. (2010) The effect of body size on the wing movements of pteropodid bats, with insights into thrust and lift production. *The Journal of Experimental Biology*, **213**, 4110-4122.

Robbins, C.T. (1993) *Wildlife Feeding and Nutrition*, 2nd ed. Academic Press, San Diego.

Robinson, W.D., Bowlin, M.S., Bisson, I., Shamoun-Baranes, J., Thorup, K., Diehl, R.H., Kunz, T.H., Mabey, S. & Winkler, D.W. (2010) Integrating concepts and technologies to advance the study of bird migration. *Frontiers in Ecology and the Environment*, **8**, 354-361.

Rosenberg, D.K. & McKelvey, K.S. (1999) Estimation of habitat selection for central-place foraging animals. *Journal of Wildlife Management*, **63**, 1028-1038.

Rosenzweig, M.L. & Abramsky, Z. (1997) Two gerbils of the Negev: A long-term investigation of optimal habitat selection and its consequences. *Evolutionary Ecology*, **11**, 733-756.

Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A, Halpin, P.N., Joppa, L.N., McClellan, C.M. & Clark, J.S. (2008) Understanding movement data and movement processes: current and emerging directions. *Ecology Letters*, **11**, 1338-1350.

Schmidt-Nielsen, K. (1984) *Scalling: Why is animal size so important?* Cambridge University Press, Cambridge.

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A. & Nathan, R. (2010) Long-distance seed dispersal. *Fruit development and seed dispersal* (ed L. Østergaard), pp. 204-237. Blackwell Publishing, Oxford.

Schurr, F.M., Steinitz, O. & Nathan, R. (2008) Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology*, **96**, 628-641.

Shanahan, M. & Compton, S.G. (2001) Vertical stratification of figs and fig-eaters in a Bornean lowland rain forest: how is the canopy different? *Plant Ecology*, **153**, 121-132.

Shanahan, M., So, S., Compton, S.G., Corlett, R., Scott, P., Studies, F., Po, M., Reserve, N., Long, Y. & Kong, H. (2001) Fig-eating by vertebrate frugivores: a global review. *Biological Reviews*, **76**, 529-572.

Shilton, L.A., Altringham, J.D., Compton, S.G. & Whittaker, R.J. (1999) Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 219-223.

Simons, A.M. (2004) Many wrongs: the advantage of group navigation. *Trends in Ecology & Evolution*, **19**, 453-455.

Smith, C.S., Epstein, J.H., Breed, A.C., Plowright, R.K., Olival, K.J., de Jong, C., Daszak, P. & Field, H.E. (2011) Satellite telemetry and long-range bat movements. *PloS ONE*, **6**, e14696.

Srinivasan, M.V., Zhang, S.W., Altwein, M. & Tautz, J. (2000) Honeybee navigation: Nature and calibration of the "odometer." *Science*, **287**, 851-853.

Steiner, I., Bürgi, C., Werffeli, S., Dell'Omo, G., Valenti, P., Tröster, G., Wolfer, D.P. & Lipp, H.P. (2000) A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiology & Behavior*, **71**, 589-96.

Stenseth, N.C. & Lidicker, W.Z. (1992) *Animal dispersal: small mammals as a model*. Chapman & Hall, London.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton.

Sun, C., Ives, A.R., Kraeuter, H.J. & Moermond, T.C. (1997) Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia*, **112**, 94-103.

Swingland, I.R. & Greenwood, P.J. (1983) *The Ecology of Animal Movement*. Clarendon Press, Oxford.

Tan, K.H., Zubaid, A. & Kunz, T.H. (2000) Fruit dispersal by the Lesser dog-faced fruit bat, *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae). *Malayan Nature Journal*, **54**, 57-62.

Tang, Z., Chen, Z., Ma, J., Zhu, G., Ma, X., Sheng, L. & Li, Y. (2010) Foraging areas of *Rousettus leschenaulti* on the Hainan Island of China. *Current Zoology*, **56**, 479-484.

Tian, L., Lin, W., Zhang, S. & Pan, Y. (2010) Bat head contains soft magnetic particles: evidence from magnetism. *Bioelectromagnetics*, **31**, 499-503.

Tidemann, C.R. & Nelson, J.E. (2004) Long-distance movements of the grey-headed flying fox (*Pteropus poliocephalus*). *Journal of Zoology*, **263**, 141-146.

Tolman, E.C. (1948) Cognitive maps in rats and men. *Psychological Review*, **55**, 189-

208.

Tous, J. & Ferguson, L. (1996) Mediterranean fruits. *Progress in new crops* (ed J. Janick), pp. 416-430. ASHS Press, Arlington.

Tregenza, T. (1995) Building the ideal free distribution. *Advances in Ecological Research*, **26**, 253-307.

Tsoar, A., Nathan, R., Bartan, Y., Altstein, O., Vyssotski, A.L., Dell'Omo, G.D. & Ulanovsky, N. (2011a) Large scale map-like navigation memory in a mammal. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, E718-E724.

Tsoar, A., Shohami, D., Nathan, R., Years, F. & Ecology, I. (2011b) A movement ecology approach to study seed dispersal and plant invasion: an overview and application of seed dispersal by fruit bats. *Fifty years of invasion ecology: the legacy of Charles Elton* (ed D.M. Richardson), pp. 101-120. Wiley-Blackwell, Oxford.

Ulanovsky, N. & Moss, C.F. (2008) What the bat's voice tells the bat's brain. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 8491-8498.

Wahaj, S.A., Levey, D.J., Sanders, A.K. & Cipollini, M.L. (1998) Control of gut retention time by secondary metabolites in ripe Solanum fruits. *Ecology*, **79**, 2309-2319.

Wakefield, E., Phillips, R. & Matthiopoulos, J. (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series*, **391**, 165-182.

Wallraff, H.G. (2004) Avian olfactory navigation: its empirical foundation and conceptual state. Animal Behaviour. **67**, 189-204.

Wallraff, H.G. (2005) *Avian Navigator: Pigeon as a Paradigm*. Springer, New York.

Westcott, D.A., Bentrupperbaumer, J., Bradford, M.G. & McKeown, A. (2005)

Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, **146**, 57-67.

Will, H. & Tackenberg, O. (2008) A mechanistic simulation model of seed dispersal by animals. *Journal of Ecology*, **96**, 1011-1022.

Wiltschko, R. & Wiltschko, W. (2003) Avian navigation: from historical to modern concepts. *Animal Behaviour*, **65**, 257-272.

Yovel, Y., Falk, B., Moss, C.F. & Ulanovsky, N. (2010) Optimal localization by pointing off axis. *Science*, **327**, 701-704.

ואפילו גדול משל העטלף. נראה שעטלף הפירות הוא "מפיץ על" בכל הקשור ליכולתו להפיץ זרעים למרחק.

למחקר זה מספר השלכות מעשיות בהקשר של ניהול משאבי טבע ושמירת טבע. לדוגמא, מצאתי שהעטלפים עפים מהמושבה לעצי הפרי ממרחקים מאוד ארוכים, ושהם מראים נאמנות לעצי פרי מסוימים. על כן בבואנו לטפל בנזקי חקלאות הנגרמים מעטלפי פירות, לא נכון יהיה לטפל במושבה הקרובה לאזור הנפגע, מפני שעטלפים יכולים להגיע למטע גם ממרחקים גדולים. בשל נאמנות העטלף לעץ מסוים, יהיה נכון יותר ללכוד את העטלפים המזיקים הספציפיים המגיעים למטע. כך ימנע נזק גדול לשאר חברי המושבה ולאורגניזמים הנוספים הקיימים במושבה. במחקר נידונה גם תרומתם החשובה של העטלפים להפצת זרעים למרחקים, החשובה לשמר אוכלוסיות עצים ברות-קיימא. יחד עם זאת, יש להתחשב גם בפוטנציאל של העטלפים להפיץ מינים פולשים.

לסיכום, בעבודה זו בחנתי מספר היבטים באקולוגיה של התנועה של עטלפי הפירות תוך שימוש בכלים מתקדמים לאיסוף וניתוח הנתונים. אנו עומדים ללא ספק על סף של עידן מלהיב שבו הטכנולוגיה מאפשרת לנו לאסוף נתונים ולענות על שאלות שלא יכולנו לענות עליהן עד היום. כיווני המשך של העבודה כוללים בירור החושים הנוספים בהם העטלפים משתמשים לצורך ניווט ארוך טווח, וכיצד משפיעה האינטראקציה החברתית בין הפרטים על השיחור למזון ויכולת הניווט.

עטלף הפירות יכול להוות חיית מודל מצוינת למחקר על תנועה וניווט בעולם החי בשל היותו נפוץ, גדול יחסית למיני עטלפים אחרים, קל לאחזקה ולאילוף, חברותי ובעל מוטיבציה גבוהה לחזור למושבה, בדומה ליוני דואר. אני מקווה שעבודה זאת היא רק ההתחלה של מחקר ארוך טווח ביצורים יפים ומרתקים אילו, בהם עוד רב הנסתר על הגלוי.

נוספים שוחררו מהר אבנון שעל שפת המכתש, והיו חשופים לאותות חזותיים מוכרים. העטלפים ששוחררו בתוך המכתש הראו בחמישה עשר הקילומטרים הראשונים של תעופתם תנועה שהייתה באופן מובהק סיבובית הרבה יותר מתנועת העטלפים מקבוצת הביקורת שעל הר אבנון שמתחילת המסלול עפו הישר למושבה. מעניין לציין שלמרות התנועה הסיבובית, כל העטלפים ששוחררו בתחתית המכתש יצאו ממנו בכיוון "הנכון" צפונה. מניסוי זה הסקתי שהעטלפים אכן נעזרים בראייה לצורך התמצאות במרחב, אך לא מסתמכים על חוש זה בלבד לניווט, וכנראה שהם נעזרים בחושים נוספים, דוגמת חוש הריח או מגנטיות.

בשני הפרקים הראשונים מצאתי כי עטלפי הפירות ניחנים ביכולת תעופה וניווט לטווח ארוך. יכולת זו מרמזת על יכולתם להפיץ זרעים למרחקים ארוכים מאוד.

בפרק השלישי, בעבודת המחקר,בחנתי את יכולת הפצת הזרעים של עטלפי הפירות ואת הפוטנציאל שלהם להפיץ מיני צומח פולש. בניתי מודל מרחבי להערכת הסתברות הפצת הזרעים למרחקים שונים, בהתבסס על יכולת התנועה של העטלפים, ומניסויי מעבר מעי שביצעתי במעבדה. מצאתי שהעטלפים יוצרים דגם פיזור זרעים מורכב שבו רוב הזרעים מופצים מתחת לעצי פרי אך גם מתחת לעצי סרק, באופן דומה, וכי בקרבת עץ מסוים ייתכנו זרעים ממספר עצים שונים. כמו כן, מצאתי שהעטלפים יכולים להפיץ זרעים למרחקים של עד כ 20 קילומטרים מצמח האם. העטלפים אינם בררניים בסוגי הפירות שהם אוכלים, ובשל העדפתם לשחר למזון בקרבת יישובים, נמצא בעבודת מחקר זו, שהם בעלי פוטנציאל גבוה להפצה של מיני צומח פולש.

מרחקי ההפצה הממוצעים והמרביים נמצאו גבוהים בהרבה מהצפוי לפי יחסי אלומטריה (Allometry), וזאת למרות שמהירות התנועה וזמן מעבר מעי היה דומה לצפוי על פי יחסי אלומטריה. הסבר לכך טמון בתעופה הימתית של העטלפים שנמצאה בפרק הראשון של העבודה. מצאתי, שעטלף הפירות מפיץ זרעים למרחקים, הגבוהים פי עשרה ממרחקי הפצה של מיני יונקים ועופות שאינם מעופפים וגודל גופן דומה לשל העטלף, ואף גדולים באופן ניכר ממרחקי הפצה הצפויים עבור ציפורים מעופפות שגודל גופן שווה

בשלב הבא יצרתי מפת אטרקטיביות שכל תא בגודל 1 קמ"ר שבה מחושבת צפיפות העצים (צפיפות גבוהה יותר מעידה על אטרקטיביות גבוהה) וערך זה מחולק במרחק מהמושבה (מרחק גבוה יותר מציין אטרקטיביות נמוכה). כך שלכל תא במפה קיים ציון אטרקטיביות אשר נורמל לערכים שבין 1 (האטרקטיביות הגבוהה ביותר) ל 0 (האטרקטיביות הנמוכה ביותר). מצאתי שהעטלפים בחרו אתרים שבאופן מובהק אטרקטיביים יותר מממוצע תאים אקראיים במרחב. עצי הפרי מאותו מין ומאותו מצב בשלות פנולוגי, אשר קרובים יותר למושבה מאשר עצי הפרי שנבחרו למאכל על ידי העטלפים, לא קיבלו ציון אטרקטיביות גבוה, באופן מובהק, מהממוצע. מצאתי גם שהעטלפים, בתעופה היממתית עפים במהירות החסכונית ביותר ליחידת זמן ולא ליחידת מרחק, וזאת בניגוד לצפוי מתעופה יממתית.

תעופה יממתית ארוכה זאת מרמזת על כך שלעטלפים יכולת ניווט גבוהה, אשר מאפשרת להם לעוף בחזרה למושבה, מאזורים רחוקים.

בפרק השני בחנתי את יכולת הניווט של העטלפים על-ידי סדרת ניסויי התבייתות. בשלב הראשון רציתי לבחון האם עטלפים מסוגלים לבחור נתיב תעופה בהתאם לאתר היעד שלהם. לשם כך העברתי עטלפים שלכדתי ב"מערת סגפים", באמצעות שקיות בד, אל גבעות גורל שמצפון לבאר שבע, מרחק של כארבעים וארבעה קילומטרים מהמושבה שבה נלכדו ורחוק מתחום שיחור המזון הרגיל שלהם. בעטלפים אלו ביצעתי אחד משני הטיפולים: שחרור מיידי אחרי ההגעה, מצב שבו העטלף רעב ויעדו הצפוי הוא עץ פרי, או האכלה של העטלף בכלוב ושחרורו סמוך יותר לזריחה, מצב שבו העטלף שבע וצפוי לחזור למושבה. נמצא שהעטלפים הגיבו כמצופה, העטלפים המורעבים עפו ישירות לעצי פרי באזור המוכר שלהם ולעומתם עטלפים שהואכלו עפו ישירות למושבתם. מכך הסקתי שהעטלפים מסוגלים לנווט בהתאם לרצונם למטרות שונות במרחב.

מטרת הסדרה השנייה של ניסויי ההתבייתות הייתה לבחון האם עטלפים משתמשים באותות חזותיים לצורכי ניווט. לשם כך הרחקתי אותם למכתש הגדול שבנגב, שם שוחררו עשרה עטלפים, בתוך המכתש, ללא אותות חזותיים מוכרים ועשרה עטלפים

זאת והוא מכשיר ה GPS הקטן ביותר בעולם שהותאם לצורכי מעקב אחרי בעלי-חיים. בנוסף נעזרתי במכשור רדיו-טלמטריה, במערכות מידע גיאוגרפיות ובכלי תכנות מתקדמים דוגמת תוכנת MATLAB.

לצורך מחקר זה עקבתי אחרי מאה עטלפים שונים, מתוכם שבעים וארבעה בעזרת מכשיר לוויני ועשרים ושישה נוספים בעזרת רדיו-טלמטריה. בנוסף ביצעתי ניסויי מעבר מעי במעבדה בשלושה עשר עטלפים נוספים. אספתי מידע על תנועת העטלף ממכשירי ה GPS למשך זמן של עד כארבעה לילות עוקבים ולרוב בתדירות דיגום של מיקום אחד לשנייה. ממכשירי הרדיו-טלמטריה אספתי מידע במשך לילה אחד ועד לשלושה עשר לילות. מיקום העטלף נקבע על-ידי טריאנגולציה בעזרת מספר חוליות, ונרשם במרחב הגיאוגרפי כל שתי דקות. כל העטלפים נלכדו ממושבה ב"מערת סגפים" שבשפלת יהודה (31^o 40' N; 34^o 54' E;) ברום של כ 250 מטר מעל לפני הים).

בפרק הראשון, בעבודת מחקר זו, מדדתי את התנועה המרחבית של עטלפים המשחרים למזון בסביבתם הטבעית ואת מידת הנאמנות של פרטים לאתר המושבה (roost) ולעצי פרי מסויימים. בחנתי גם כיצד המשתנים בנוף משפיעים על תנועת השיחור למזון של העטלפים והאם קיים דגם בהעדפת אתרי השיחור.

מצאתי שהעטלפים מראים נאמנות בינונית עד גבוהה לאתר המושבה .העטלפים מראים דגם קבוע של שיחור למזון שמתאפיין בתעופה יוממתית (Commuting) ארוכה, עד עשרים וחמישה קילומטרים מהמושבה, בתעופה גבוהה (בממוצע 103.8 מטר מעל לפני הקרקע), מהירה (ממוצע של 9.28 מטר\שניה) וישרה (ממוצע מדד יישורת של 0.92) לעץ פרי שבסביבתו הם נשארים, רוב שעות הלילה, עד לשובם למושבה.

העטלפים מראים נאמנות גם לנתיב התעופה ולעצי הפרי שמהם הם ניזונים. כמו כן מצאתי שמבנה הנוף משפיע על דגם השיחור למזון של העטלפים ברמת הפרט וברמת האוכלוסייה. דגם הפיזור של אוכלוסיית העטלפים דומה לדגם פיזור העצים במרחב ושעטלפים מעדיפים עצים שקרובים יותר, יחסית, למושבה.

תקציר עבודה

תנועה היא מרכיב הכרחי במערכות חיים רבות עלי אדמות. בעלי חיים נעים במרחב לצורך שיחור למזון. חיה המשחרת למזון צריכה לקלוט מידע מסביבתה כדי להחליט מתי ולהיכן לנוע במרחב, על מנת להשיג מזון באופן יעיל משיקולי זמן ואנרגיה. יחסי צומח - בעלי-חיים מהווים מרכיב חשוב במערכות היחסים האקולוגיות בעולם. יחסים אלה קובעים, בדרך כלל, את הפיזור המרחבי של הצמחים ושל אוכלי הצמחים, ובאופן חלקי את הפצת הזרעים במרחב.

עבודת מחקר זאת מורכבת משלושה חלקים שונים שהחוט המקשר ביניהם הוא האקולוגיה של תנועה של עטלף הפירות (*Rousettus aegyptiacus*).

בפרק הראשון אני בוחן את התנועה המרחבית של עטלפים בהקשר של שיחור למזון וכיצד מבנה הנוף ופיזור עצי הפרי במרחב משפיעים על תנועה זו. בפרק השני אני בוחן את יכולות הניווט של העטלף למרחקים ארוכים ומאזורים שבהם לא היה בעבר, וזאת על ידי סידרת ניסויי התבייתות (Homing). בפרק השלישי אני בוחן כיצד התנועה המרחבית ואופן השיחור למזון של העטלף, משפיעים על יכולת הפצת הזרעים שלו, וכיצד עטלף הפירות מהווה סוכן הפצה למרחק של זרעי עצים ממוצא טבעי וממוצא זר.

במחקר זה אני עושה שימוש במספר שיטות עבודה חדשניות שנועדו למדוד ולכמת את התנועה המרחבית של העטלפים, השיחור למזון, יכולות הניווט, ויכולתם להפיץ זרעים במרחב. השיטות הנכללות בעבודה זאת כוללות שימוש במכשור ביו-טלמטרי מתקדם, ניסויי התבייתות, ניסויי מעבדה, מודלים ממוחשבים ושיטות סטטיסטיות מתקדמות לניתוחים מרחביים.

בעבודה אני נעזר במכשירי איכון מרחבי (GPS) זעירים המוצמדים לעטלפים לצורך איסוף מיקומם במרחב באופן מדויק ובתדירות גבוהה מכל מכשיר אחר ששימש עד כה למחקר בתחום זה. ההתקדמות הטכנולוגית במזעור מכשור GPS, אפשרה לראשונה להצמיד לגב העטלף מכשיר GPS הכולל אוגר נתונים. מכשיר זה הותאם במיוחד לעבודה

עבודה זו נעשתה בהדרכתו של פרופ' רן נתן

שיחור מזון ויכולות הניווט של
עטלף הפירות (*Rousettus aegyptiacus*)
ותרומתו להפצת זרעים

חיבור לשם קבלת תואר

דוקטור לפילוסופיה

מאת: אסף צוער

הוגש לסנט האוניברסיטה העברית בירושלים

טבת התשע"ב