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היבטים באקולוגיה של תנועת נשרים:

המנגנונים המעצבים את דגמי שיחור המזון והשלכותיהם האקולוגיות

Movement Ecology of Vultures: Foraging Patterns, Their Underlying Mechanisms and Ecological Consequences

הריני מאשר את הנושא ואת התוכנית, ומסכים להדריך את המועמד בביצוע עבודה זו:

פרופסור רן נתן

2 עמ'

Abstract

Movements of organisms affect the fate of individuals and the dynamics of ecosystems. Identifying movement patterns and their underlying mechanisms is essential for understanding these dynamics, for developing effective management plans, and for coping with environmental threats such as the spread of infectious disease.

Vertebrate scavengers in general, and vultures in particular, play an important role in many ecosystems, providing sanitation services through removal of carcasses. Yet, they may also disperse diseases in the same manner. Carcasses are typically unpredictable in time and space, thus, vultures forage socially and over huge areas. This unique foraging behavior, together with the high conservational priority of the vultures, makes them particularly suitable for studying the links between patterns and mechanisms of animal movement.

In this study, I propose to examine how external and internal factors (social interactions, resource distribution, site-fidelity and species niche) interact to determine movement patterns and foraging of vultures. Furthermore, I will explore the consequences of these patterns on foraging efficiency, as well as on the role of vultures in spreading disease pathogenes. I hypothesize that both internal (e.g. site fidelity) and external factors (e.g., resource predictability) will affect the properties of the foraging movements in a predictable manner, and therefore influence the foraging efficiency and ecological functionality of the vultures. To test these hypotheses, I will combine field manipulation of resource distribution, field observations at roosts and feeding sites along with high resolution GPS tracking and behavioral data obtained from momentary acceleration sensors.

Fieldwork will be done in two semi-arid regions, with *Gyps fulvus* (in southern Israel), *G. africanus* and *Torgos tracheliotus* (in the Etosha National Park at Namibia). Movement indices as step size and track tortuosity will allow comparison of the vultures movement tracks, especially during foraging search phase. Currencies of foraging efficiency (e.g., resource finding and consumption rate) will be used to test the consequences of the movement patterns. Initial results from GPS tracks in Namibia and Israel demonstrate the feasibility of the proposed methods and the advantage of integrating positioning and behavioral data. The results of this study should contribute to effective management of vultures in both regions and provide insights into the mechanisms shaping animal movements and foraging efficiency.

Background:

Movement is a fundamental feature of life, playing a major role in determining ecological and evolutionary processes (Dingle 1996, Dingle & Drake 2007). A major challenge in movement research is linking the movement patterns to their underlying mechanisms (Nathan et al. 2008). The linking is essential for understanding ecosystem functioning and community dynamics, for developing effective management plans, and for coping with environmental threats such as invasive species and spread of infectious disease (Webster et al. 2002, Williams et al. 2002). Thus, a mechanistic approach, in which the mechanisms underlying movement patterns are identified, should enable elucidating the general rules governing the role of organismal movements in determining ecosystem and community dynamics (Nathan et al. 2008).

Recent progress in our ability to collect movement data by means of innovative technologies such as miniaturized GPS tags, has set the stage for the development of new statistical methods for analyzing movement paths (e.g., Patterson et al. 2008, Bartumeus & Levin 2008). Progressing beyond phenomenological descriptions is challenging for three main reasons. First, identifying the movement goal (i.e., the specific motivation to move at a curtain time) is challenging in many cases. Movement can be motivated by a variety of proximate (e.g., finding mate, food or shelter) and ultimate goals (fitness consequences, e.g., reproduction, maintenance and survival, respectively). The identification of distinctive movement phases, defined as sequences of steps and stops intended to fulfill the same set of goals (Nathan et al. 2008) such as a foraging bout or a return-to-the-roost bout, is thus the essential first step towards understanding the underlying mechanism.

A second general challenge in developing a mechanistic understanding of movement is to identify the set of internal traits and external factors that play a significant role in shaping the movement path. According to the movement ecology framework (Nathan et al. 2008), these can be classified into (a) the internal state of the focal individual (e.g., its body condition and previous experience); the traits and trade-offs determining its (b) motion capacity (the ability to move) and (c) navigation capacity (the ability to decide when and where to move in response to information about the environment); and (d) the set of external factors such as social interactions (group members, competitors and other conspecifics) and resource distribution.

The third major challenge is to quantify the fitness consequences of different movements, especially for long-lived species with delayed maturity and a long generation time. Short-term currencies such as foraging efficiency and energetic intake often serve as proxies (Pyke et al. 1977, Ydenberg et al. 1994). Related currencies such as resource depletion rate and the rate of individual's displacement from a given point, can be used to elucidate how foraging behavior affects higher hierarchal levels such as ecosystem functioning and structure (DeVault et al. 2003). For instance, carcass removal rate depends, among other factors, on the foraging efficiency of scavengers, and can affect the rate of disease spread (DeVault et al. 2003, Sekercioglu 2006).

Vertebrate scavengers play an important role in many ecosystems, maintaining energy flow in food webs, providing sanitation services through carcass removal, but also dispersing diseases in some of these ecosystems. Vultures are the only obligate scavengers and the most prominent ones in many ecosystems (DeVault et al. 2003, Ruxton & Houston 2004, Sekercioglu 2006). Since availability of carcasses is typically unpredictable in time and space, vultures foraging efficiency relies on high mobility and on social foraging strategies, allowing the vultures to collectively scan vast areas. The typical large size of a carcass negates the potential disadvantages of social foraging (i.e., many carcasses are too big to be consumed by a single scavenger) (Houston 1974, Prior & Weatherhead 1991, Buckley 1996 Ruxton & Houston 2004). Like many other large-bodied birds, vulture populations suffer from acute decrease due to anthropogenic interference (Leshem 1985, Prakash et al. 2003, Green et al. 2004). The unique combination of high mobility, complex social foraging and high conservational priority, together with the relatively large body size of the vultures (facilitating the use of tracking techniques), makes them particularly suitable to explore the links between patterns and mechanisms of animal movement. The fact that vultures are relatively 'predator-free' minimizes the component of risk in the foraging cost-benefit trade-off and allows for a better use of foraging efficiency proxies.

Research Goals:

The proposed research will focus on the movement pattern of vultures and address two fundamental questions about animal movement:

1. How internal and external factors interact to determine movement patterns of foraging vultures? Specifically, I will look at the effects of information-sharing through social interactions, social dominance, resource predictability and breeding status (i.e., central place foraging during nesting period) on foraging behavior: the length and duration of foraging bouts and their tortuosity (defined as the ratio between the travelled distance and the net displacement).
2. What are the consequences of movement patterns at two levels: (a) The foraging efficiency of an individual (the time elapsed and the distance traveled between feeding events and the

resource intake rate. (b) At the ecosystem level, the probability of carcass detection and time until discovery, the carcass-removal rate and the disease spread rate.

I shall follow the Lagrangian (individual-based) approach of acquiring high quality movement and behavioral data on vultures through a combination of GPS-tracking technology with an independent momentarily acceleration sensor (ACC). This will be completed by data of visits to feeding stations from RFID (Radio-frequency identification) tagging of many individuals. As descriptors of the movement path, I will use several commonly used indices (e.g., tortuosity, step length and kurtosis of the turning angles) (Bovet & Benhamou 1988, Patterson et al. 2008). The probability of food patch discovery and time until discovery, time and traveled distance between feeding events and food intake rate will be used as general currencies for foraging efficiency possibly corrected for estimators of energy expenditure based on data from the ACC.

Hypotheses, predictions and justifications:

For the purpose of this study, I hypothesize that movement phases with distinct objectives (e.g. the search phase) and different behavior modes (e.g., feeding or resting) can be identified by the various movement descriptors and by the ACC sampling, respectively. These working hypotheses will be validated at the early stages (as can be seen in the preliminary results section). Under these assumptions, I hypothesize that the movement pattern during foraging search phase and consequently the foraging efficiency itself both change according to the following factors: (Hypothesis 1, hereafter simply H1) information on resource location available to individual from following other individuals, (H2) the spatial and temporal predictability of food resources, (H3) the site-fidelity of the vulture to its roost (i.e., the probability of returning to the same roost site; varying in time according to the breeding status) and the (H4) species niche within the vultures community. In addition, I hypothesize (H5) that the social rank of the individual will affect its movement. Dominants, (presumably adults) may be either 'late arrivers' waiting for other conspecifics to find a carcass and then overtaking them or 'pioneers' that are more likely to find a food patch (and are hence the first arrivers). Finally, I hypothesize that (H6) vultures' movements will affect the dynamics of disease spread (specific predictions below).

The following predictions (P1-P6) state the trend of the prediction-specific explanatory factor that will improve foraging efficiency and induce movement directionality during the foraging search phase (i.e., will give rise to less tortuous movement paths, higher mean velocity):

P1. Previous information: Higher level of social information sharing. Vultures share information on carcass location (Houston 1986, Cramp 1988, Mundy et al. 1992, Buckley 1996). Information can be shared with conspecifics or with other species, passively or actively, through local enhancement at a carcass or as an information center in the communal roost. Regardless of the mechanism, information sharing is predicted to increase the resource detection range (as compared with solitary foraging), to minimize search time, and to give rise to more directional movement and to more efficient foraging. Therefore, vultures foraging from communal roosts will have more directional movements, and a higher foraging success than vultures searching alone or from an occasional roost, or that of the first finder of a carcass (Buckley 1996).

P2. Resource predictability: Higher predictability of food resources in space and time. The search phase will be minimized when carcasses are at a predictable location. Therefore, vulture movement to a known feeding station will be directional, whereas movement to carcasses supplied at random sites will be more tortuous and with a longer search phase.

P3. Site-fidelity: Lower site-fidelity. Vultures tend to return to one primary roost site (or to a limited set of alternative sites) over a season or even longer periods. Site fidelity may vary throughout the year. During the breeding season, adults rearing their young can be regarded as obligate central-place foragers (O-CPFs). Otherwise, out of the breeding season, vultures return to a limited number of interchangeable roosts, and can be considered as "facultative CPFs" (F-CPF). Juveniles and non-breeding adults may be considered as F-CPFs all year round. While F-CPFs may 'drift' further away when searching for food, for O-CPFs, the costs of straying from the roost are higher (especially when food items have to be transported back to the roost). Hence, during the search pbase, the net displacement and directionality of an O-CPF are expected to be less than an F-CPF. The search of the former is expected to be more tortuous and spatially limited than that of the latter. Therefore, during the nesting period, and especially during the chick provisioning period, the vultures foraging movements are expected to be more tortuous than those of non-breeding adults.

P4. Interspecific differences- *Gyps spp.* (*G. fulvus*, Griffon vulture; and *G. africanus*, White-backed vulture) vs. *Torgos tracheliotus* (Lappet-faced vulture). Diet differences between the *Gyps* spp. and the Lappet-faced vulture may lead to differentiation of the search pattern. While Lappet-faced vultures are larger and more dominant, they are usually outnumbered by White- backed vultures at the carcass (Mundy et al. 1992). Therefore, Lappet-faced vultures may act as a pioneer species in the Etosha National Park, similarly to the role turkey vultures (*Cathartes aura*) play among new world vultures (Prior & Weatherhead 1991, Buckley 1997). Consequently, White-backed vultures may forage at faster speeds and at higher elevations (Buckley 1997). Moreover, higher population density (Mundy et al. 1992) may also allow

Gyps to share more information and to improve their efficiency and directionality. In addition, site fidelity and flight duration may differ between species.

P5. Social dominance. Dominant individuals will arrive at carcasses before inferior individuals (probably juveniles and inexperienced birds) and will outcompete them in accessing the carcass (Bose & Sarrazin 2007). Alternatively, dominants may be "late arrivers" (*sensu* Buckley 1996) and have a similar role to the role black vultures (*Coragyps atratus*) fill among new world vultures (Prior & Weatherhead 1991, Buckley 1996) but within the species scale. If the latter supposition is true, then dominants may fly higher and look for descending vultures instead of for stationary carcasses, and an association between directional foraging flights at high elevation and a late order of arrivals is expected (Buckley 1997).

P6. Disease transmission. Vulture roosts and perch points are expected to function as local infectious zones where high pathogens concentrations are found (Houston & Cooper 1975, Hugh-Jones & de Vos 2002). This is expected to be more pronounced in roosts used immediately following consumption of infected meat (with relevant time span depending on the pathogens retention time by the vulture).

Methods:

The proposed research will combine intensive fieldwork in two semi-arid regions (Israel and Namibia) with analytical and modeling work. The core method of the research is based on GPS tracking of movement with accompanying observation and field manipulations to test the different factors.

Study species and sites: Vultures are large obligatory scavengers common in various habitats in the old world (Cramp 1998, Mundy et al. 1992). Soaring flight depends on rising air-currents. Vultures tend to depart from the colony/roost in groups, but individuals may search for food solitarily, visually locating carrion of medium to large mammals, especially ungulates (Cramp 1988). High-velocity gliding provides a signal for many individuals to congregate on a carcass, often showing aggressive interactions (Cramp 1988).

In Israel, the local Lappet-faced vulture subspecies (*T. tracheliotus negevensis*) has became extinct by the mid 1980s. The Griffon vulture is of major conservation concern with population also at high risk mostly because of exceptionally low breeding success (Nathan 1989, Freund et al. 2004) and large inter-annual fluctuations in population size (Freund et al. 2004; O. Hatzofe, pers. comm.). According to the Israel Nature and National Parks Protection Authority (INNPPA), approximately 240 Griffon vultures currently inhabit the southern part of Israel, most of those who breed in Israel (~50 pairs), breed and roost in a few main colonies throughout the Judean and Negev deserts, while others are mostly winter visitors from adjacent countries (O. Hatzofe, pers. comm.). Additional breeding colonies of up to a few tens of pairs are also located in the northern parts of the country (the Golan Heights and the Galilee). Supplemental feeding stations are routinely operated by the INNPPA providing the means to monitor and capture vultures.

Overall, a small population size, although being problematic from the conservation point of view, is advantageous from the scientific point of view by facilitating the marking of a significant proportion of the population. Observations in Israel recorded frequent long-distance forays of vultures of up to 90 km and occasionally up to 280 km in one day (Bahat 1995, 1998). The very large foraging range of vultures dictates a large study region. We selected southern Israel over northern Israel because it is relatively unoccupied and undisturbed by humans, and severe poisoning events are less frequent than in the north (Freund et al. 2004). In addition, the low food availability in the southern part of the country entails a higher reliance of the population on food supplements food; hence our experimental manipulations are more likely to succeed.

Some components of the fieldwork will be done in the Etosha National Park in northern Namibia (here after simply Etosha), a 22,915 km^2 reserve with savanna vegetation and high wildlife diversity. Yearly outbreaks of anthrax (*Bacillus anthracis*) occur at the central districts of Etosha, mostly towards the end of the rainy season (February- April) (Lindeque & Turnhull 1994). Because vegetative *B. anthracis* cells sporulate within 1-2 days after host death, scavengers were suggested as potential transmitters of the bacterial dispersive forms, potentially creating new local infectious zones of anthrax and contributing to disease transmission (Lindeque & Turnbull 1994). This part of the research will be done in collaboration with Prof. Wayne Getz and his research group at the University of California, Berkeley, studying different aspects of the anthrax ecology in Etosha. Other projects of the group include monitoring of feces and soil at vulture roosts for presence of *B. anthracis* and studying seasonal movements of ungulates in the park. These projects may provide valuable complementary data.

The White-backed vulture is common in Etosha, aggregating in large numbers (of up to 70-150) around carcasses. Lappet-faced vultures are also common in the rejoin but in smaller numbers (Mundy et al. 1992). Both species roost and nest on trees in the park and adjacent farms (W. Versfeld, pers. comm.).

Capturing and marking: free-ranging birds will be captured using two methods: (1) A standard walk-in trap, where vultures are attracted by a bait and lure birds to a large cage whose structure enables entrance only. This method is applicable in Israel, where vultures are used to feeding at permanent feeding stations. (2) A leg-hold trap (Victor #3 soft catch) concealed around a bait carcass. This method is suitable for naturally occurring or randomly located carcasses.

Captured birds will be tagged with patagial tags (tags on the wing membranes) and color rings to allow field identification over long periods. Mass and morphological measurements, as well as blood and feathers samples will be taken from all captured individuals to determine age, body condition, sex and possibly genetic relatedness. In Israel only, RFID tags will be used to allow later identification and monitoring of presence in feeding station (Gibbons & Andrews 2004).

Telemetry tracking: GPS-ACC tags (E-OBS Telemetry, Germany) will be deployed on some of the captured birds. These tags provide accurate movement tracks in fine temporal resolution (e.g., every few minutes for few months period). Additionally, the tag has an independent acceleration sensor (ACC) that measures momentarily acceleration values at three perpendicular axes in very high accuracy and temporal resolution (e.g., at 3 Hz for 30 s every 10 min). Behavioral modes and possibly also energetic expenditures can be inferred from the acceleration data (Scheibe & Grosmann 2006, Wilson et al. 2006, 2008). Data is stored onboard and can be downloaded through radio communication from a distance of up to a km. Additionally, a built-in radio transmitter (VHF transmitter) facilitates locating and tracking the tagged bird in the field. These GPS tags are state-of-the-art technology, and I believe that the unique combination of high resolution data together with some behavioral (and perhaps also energetic) data can provide a powerful tool and facilitate an integrative research about the factors shaping birds movement and ecology. **Currently, six and nine transmitters are already in use at Israel and Etosha, respectively. Within several weeks (at Israel) and months (at Namibia), five and ten additional transmitters will be deployed, respectively**. Furthermore, I'm hoping to obtain additional funding to allow placing 20-30 more transmitters in Israel, contributing to the generality of the results and possibly allowing the exploration of few more hypothesis as the effect of age and learning on movement pattern and foraging efficiency. It is important to emphasize that the research described in this proposal is independent of our success in raising these additional funds.

Track surveys: Tracks downloaded from the GPS tags will be examined to identify points of interest where vultures landed in other place than their permanent roosts or feeding stations (information of arrival at feeding station is acquired from RFID tags also). Accessible points will be surveyed in the field to determine vulture potential activity at the spot. The results will be combined with the behavioral data from the ACC to validate our ability to identify non-observed feeding events of tagged vultures, and hence to accurately determine foraging efficiency. For instance, remains of a carcass at the surveyed site, verified with feeding behavior documented by the ACC, will be considered as a feeding event.

Food manipulation: The INNPPA invests many efforts in feeding vultures, providing carcasses mainly in permanent feeding stations and creating a situation where food is relatively abundant and predictable in space. I plan to manipulate resource availability to produce an unpredictable scenario. The permanent feeding stations will be replaced by experimental stations at random locations. Confounding effects of uncontrolled naturally-occurring carcasses are rather infrequent in the southern region and are being ordinarily monitored by the INNPPA through regular field surveys and vulture observations. Altogether, I plan to do 30-50 trails of a randomly-located carcass, to achieve a sufficient sample size to compare with arrival at feeding stations. Experiments will be carried out during non breeding season (August- December), over 2-3 years, as a sequence of trials (e.g., once in five days for a month and a half), in order to allow the vultures to become used to the new situation.

Field observations: (1) At feeding sites: Direct observations will be conducted at sites of naturally available and artificially supplied carcasses. 'Time till arrival', arrival times intervals and arrival directions will be monitored. Dominance, defined as individuals replacing others around a carcass, or initiating an aggressive interaction elsewhere (Mundy et al. 1992, Bose & Sarrazin 2007) will be determined, especially for GPS tagged individuals. Presence of wing-tagged and RFID tagged individuals will also facilitate behavioral recording and enable applying mark re-sight methods for assessing population density. In Israel, the small population size and the intensive marking efforts of the INNPPA increase the feasibility of this method since **in many occasions 40%-60% of the vultures feeding at a feeding station are marked** (O. Hatzofe, pers. comm). **(2) At nesting sites:** Chick provisioning behavior of tagged birds will be monitored. During the vultures breeding season, I will acquire nest locations from the GPS data and conduct observations on the chick provisioning rate (food items provided to the nestling per time unit). The relevant time frame of feeding at the nest is 120 days, sometime with occasional feeding elsewhere later on (Mundy et al. 1992). The amount of observation days per nest depends on the final number of tagged birds in the breeding colony. Setting a goal of 8-10 nests with a bi-weekly half-day seems to be a feasible effort.

Overall, GPS tracking will be done in both regions, but other methods are relevant only for one of the two regions. For instance, the examination of P6 by soil and feces samples for *B. anthracis* spores will be done only in Etosha, and food manipulation is feasible only in Israel (Table 1). Predicted effects of the different studied factors on the response variables and the relevant methods are summarized in (Table 2). See (Appendix 1) for potential problems with the suggested study.

Data analysis: Data analysis will be done by Matlab, BioMove (currently being developed in the Movement Ecology laboratory) and Geographic Information System (GIS) to examine the properties of the recorded movement tracks. To analyze these properties, I shall split track to time-discrete movement phase, according to behavioral, physiological or external attributes. Each phase will be segmented into equal time steps according to the temporal resolution of the sampling. For each phase, I will compute numerous statistical descriptors such mean and variance of step length, tortuosity and turning angle kurtosis (Benhamou & Bovet 1992, Benhamou 2006).

Different functional forms will be fitted to the observed histograms of step length, turning angles and other indices, to test the effect of influencing attributes like resource predictability and the social context. To test the effect of level of social interactions, I shall identify "foraging groups" by analyzing the temporal sequence of individuals arriving at a carcass, and arrival direction if possible (Buckley 1997, Bose & Sarrazin 2007). Then I will use a correlated random walk approach, calibrated with data obtained from the field observation and tracking, to model the importance of the different factors and especially the social information-sharing (which is not manipulable), its effect on foraging efficiency and carcass detection probability.

Foraging currencies as resource finding and consumption rate, time and distance from last feeding event will also be used as the response variable in the statistical model. Behavioral data from the ACC recordings will be classified to activity modes (e.g., eating and resting) using a canonical discrimination analysis based on various statistics extracted from the ACC measurements characterizing the different modes (Scheibe & Grosmann 2006).

Research plan:

During the first field season at Etosha the capturing and tag-fitting protocols have been established, and the first bunch of transmitters was deployed, both there and at Israel. The remaining 'Israeli' tags will be deployed in within few weeks.

2008	Nov- Dec	Preparation for field season in Etosha
2009	Jan- Feb	A field season in Etosha: the second phase of GPS tagging and carcass observations.
2009	Mar- Aug	GPS Track surveys in Israel accompanied by carcass and nest observations.
2009	Aug- Dec	The second phase of GPS tagging in Israel. Food manipulation

		and carcass observations.
2010	Jan- Aug	GPS Tracks surveys in Israel accompanied by Nest observations.
2010	Sep- Dec	Continue of GPS Track surveys in Israel accompanied by further food manipulation and carcass observations.
2011	Jan- Jun	Data analysis and movement tracks classifications.
2011	Jul- Dec	Thesis writing.

Preliminary results:

The core method of this study relies on the ability to obtain high resolution tracks of free-ranging vultures with GPS and ACC data. The feasibility of this method is proven by the preliminary results presented in the following paragraphs. To date, GPS-ACC tags were fitted to nine vultures at Etosha, of which data has already been downloaded from five (Table 3). These tracks, range between two weeks to more than five months, with GPS and ACC sampling intervals of 2 min and 10 min, respectively. Additionally, seven vultures where tagged in Israel (five of them recently- mid October), from f which data was downloaded from two.

Initial attempts to explore the tracks with ground surveying also established the method's effectiveness. Roosts and suspected feeding points revealed clear signs of vulture activity, e.g., feathers and droppings at roost sites or carcass remains at feeding sites. Other methods included in this study (e.g. carcass and nest observations) were done in previous studies in Israel (Goell 2003, Court 2004) or elsewhere (Prior & Weatherhead 1991, Bose & Sarrazin 2007).

Examples of movement tracks demonstrate the ability to identify the relative importance of different roost sites and site fidelity (figure 1). The power of possible coupling between movement track and ACC behavioral data is demonstrated by an incident where a tagged vulture was observed in the field (figure 2), and for a daily track where behavior is inferred from the ACC data and GPS location (figure 3). See (Appendix 2) for suggested titles of publications that may follow this study.

Tables and Figures:

method	*Site*
Telemetry tracking	Israel, Namibia
Track surveys	Israel, Namibia
Food manipulation	Israel
Feeding site observations.	Israel, Namibia
Nesting sites observations.	Israel
Feces and soil sampling	Namibia

Table 1. Summary of methods by their planned study site.

	Methods of quant.	Response variable	1 Social info-sharing	2 Resource predict.	3 Site fidelity (chick provisioning)	4 *Gyps* vs. *Torgos*	5 Social dominance
Movement properties	Path analysis	Speed	+	0	+	-	0
		Tortuosity	-	-	+	0	-
		Height	+	-	0	+	+
Foraging efficiency	ACC data, Ground survey, Path analysis, RFID tags	Time from last feeding	-	-	-	-	+
		Flight distance from last feeding	-	-	-	-	-
		Time till carcass detection	-	-	0	-	0
Methods for testing the hypothesis			Modeling roost analysis	Field mani-pulations	Nest observations	Path analysis	Carcass observation RFID tags

Table 2. Predicted effects of the studied factors on the response variables and methods for assessing these effects and measuring the response variables. For each of five hypotheses, the expected trend in the measured variable for increase in the explanatory factor is given (+positive, - negative, 0- unknown). For instance, higher resource predictability, implemented by field manipulations, is predicted to decrease tortuosity and height of search flights as well the three currencies of foraging efficiency. The effect on flight speed is unclear.

Species	*Region*	*Deployment date*	*Data downloaded until*	*Track Duration*
WBV	ENP, Namibia	28/Mar/08	9/May/08	1.5 months
WBV	ENP, Namibia	31/Mar/08	27/Apr/08	1 months
WBV	ENP, Namibia	28/Mar/08	16/May/08	1.5 months
LFV	ENP, Namibia	7/Apr/08	16/Sep/08	5 months
WBV (juv.)	ENP, Namibia	6/Apr/08	20/Apr/08	2 weeks
GV	Carmel, Israel	31/Jul/08	17/Sep/08	1.5 months
GV	Negev, Israel	19/Aug/08	1/Oct/ 08	1.5 months

Table 3. Downloaded vulture tracks with GPS sampling interval of 2 min and ACC sampling interval of 10 min. WBV- White-backed vulture. LFV- Lappet faced vulture. GV- Griffon vulture. ENP- the Etosha National Park.

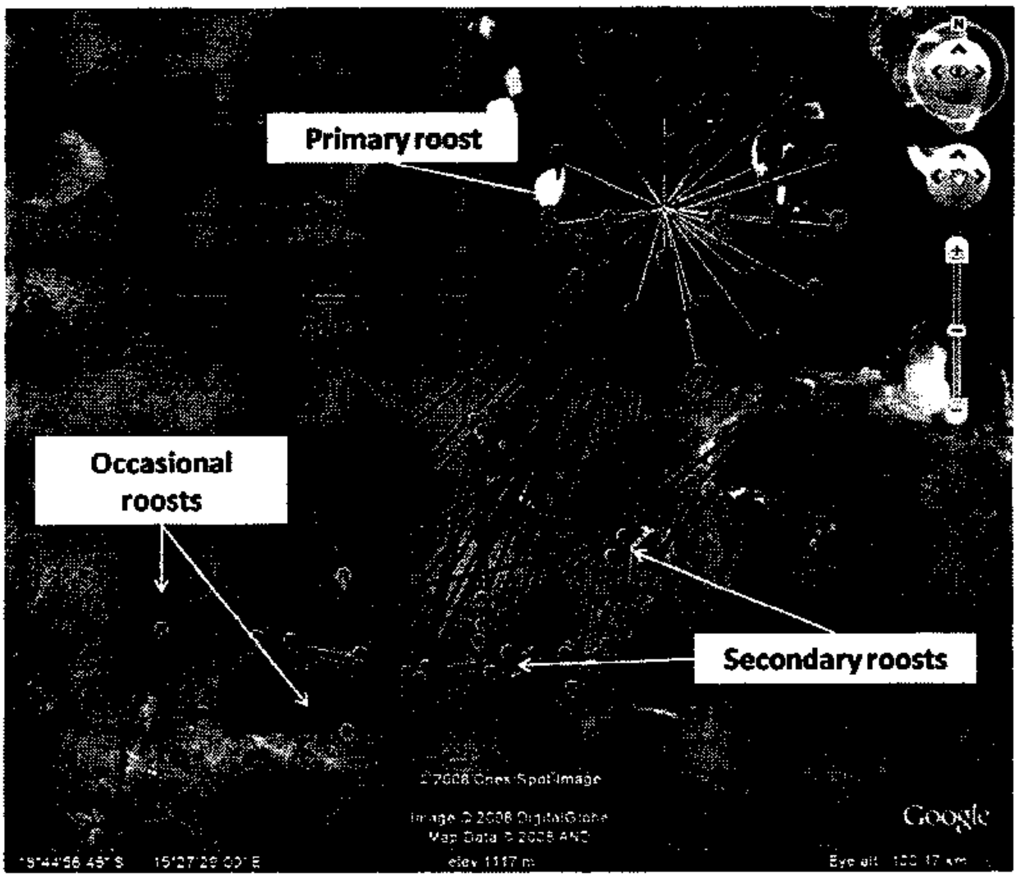

Figure 1. Roosts used by a Lappet-faced vulture during the first three month of the tracking period. Icons are a single night use of a roost site, connected in successive order by the black solid line. The primary roost in the north has been used over 24 nights out of the 87 tracking days. Other roosts were used either for few nights (secondary roosts), or just once (occasional roosts).

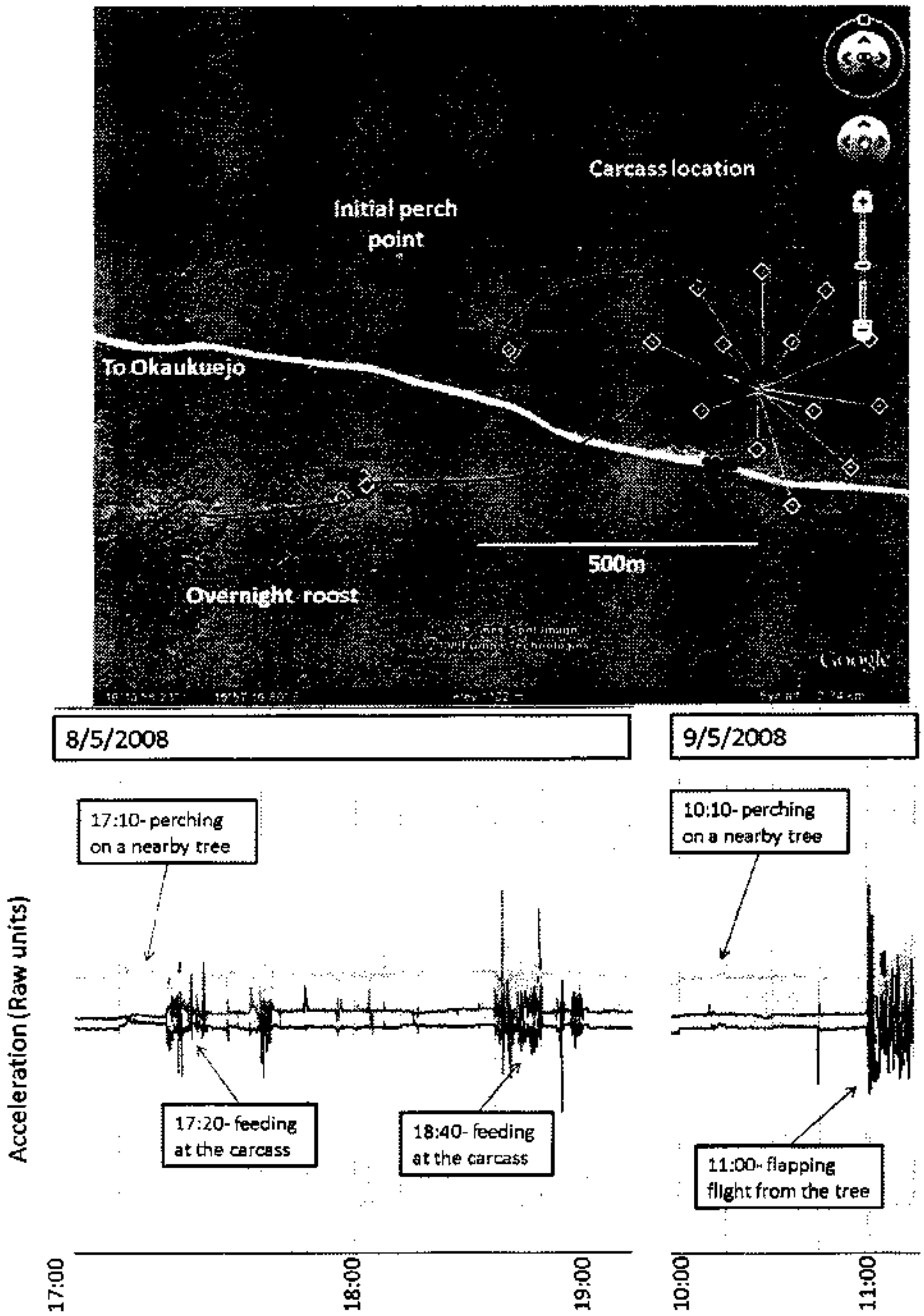

Figure 2. Movements and ACC measurement of an observed White-backed vulture. (A) Movements: The bird was located perching nearby a zebra carcass, and later landed at the site itself. The vulture was located again on the following morning after roosting on a tree. The solid line presents interpolation between sampling points at 2 min intervals. Note that the initial perch point, the carcass (feeding) location and roost site include many spatially overlapping points (presented in expanded mode for the carcass location only). (B) ACC measurements: every 10 min a 50 sec interval with 166 measurements for each axis is sampled (separated by vertical lines). The text insets show activities observed in the field.

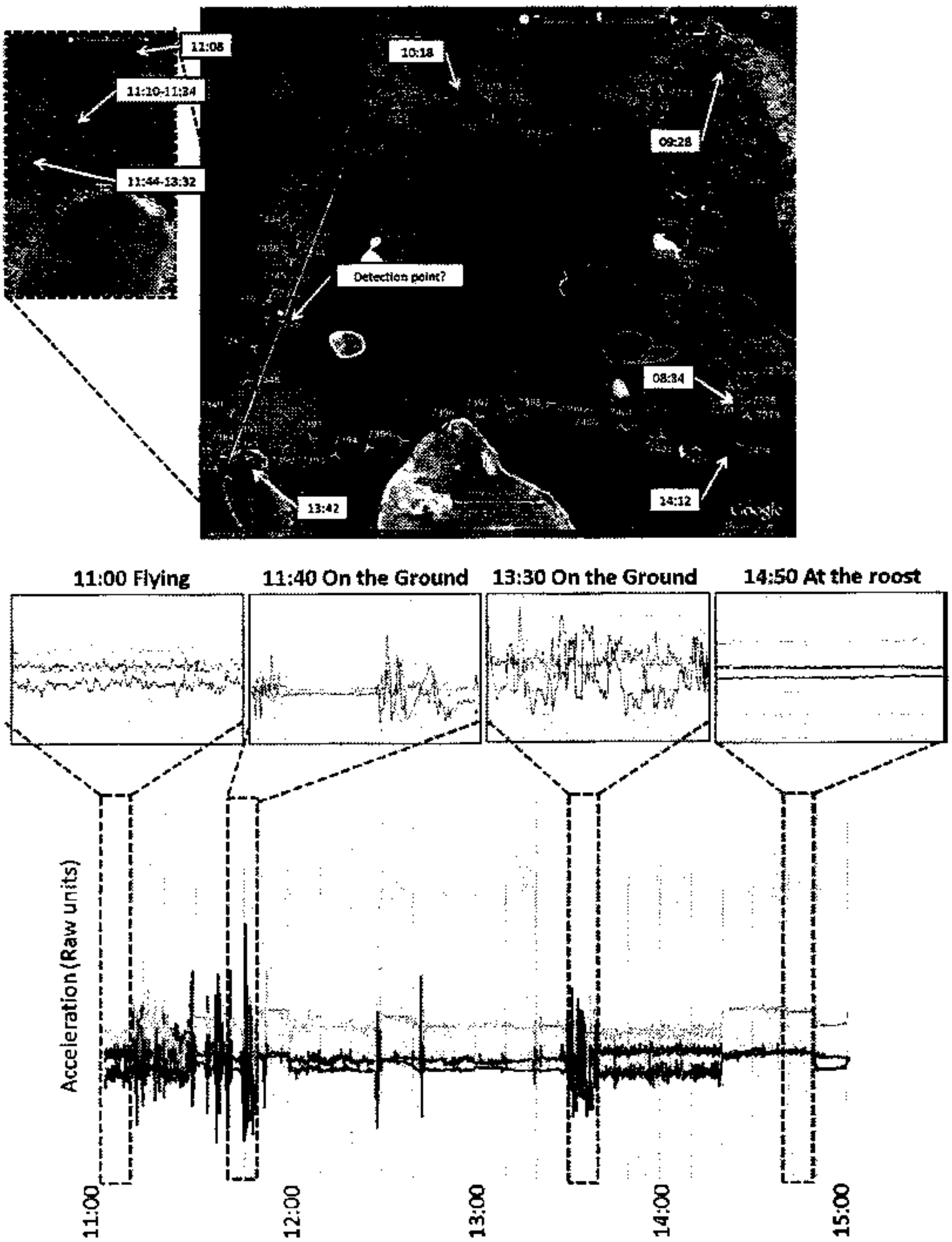

Figure 3. A movement track and ACC measurements of a White-backed vulture during a single day. (A) A day track: The bird left the roost at around 8:30, and made a non-stop flight until it landed around 11:30. At 13:30 the vulture flew directly to the roost site. 'Plain' icons represent flight (speed above 4m s^{-1}) with appropriate instantaneous heading direction. 'Triangles' represent stationary locations. The inset shows the ground stops. (B) ACC measurements (see figure 2): the intensive activity during stopping may suggest bird was feeding at the site (vulture was not observed). If true, the preceding fast and direct flight could be an approach phase after resource was located (either directly of via local enhancement).

Appendix 1. Expected problems:

The planned study relies on the assumption that high resolution movement tracks can be obtained and analyzed. Any difficulties in achieving this goal may impair the feasibility of the study. Acquiring the data depends on the ability to capture and tag birds from all species. Relocating the vultures at every given time interval and approaching them to a suitable downloading distance is also essential. While re-sightings are common in Israel, vultures may leave the focal region making this task impossible. From my experience, this problem is more acute in Etosha. To overcome this obstacle, I must rely on intensive search efforts that will be expanded to surrounding farms if necessary, and to aerial survey if needed.

A second challenge is the ability to document the activity of tagged bird, both for generating the "key" for the ACC interpretation and for determining social dominance. To some extent, the former can be done by observing captive vultures. Although not all behavioral modes may be encountered in captivity (e.g. fighting on a carcass is unlikely to happen) these observations can still increase the generality of this key. The high reliance of the Israeli vultures on feeding stations and the presence of observation points (hides) at some of those stations may facilitate the latter. If the proposed methods will be more time consuming than expected, the observations at nesting sites and tracks survey can be minimized and identification of feeding events and of chick provisioning events will be inferred from the movement tracks analysis alone.

Appendix 2. Suggested titles of publications:

- Interspecific comparisons of vulture tracks and foraging efficiency: Movement differences associated with ecological role versus landscapes features.
- The effect of resource predictability and social information-sharing on search behavior, food detection and foraging efficiency of vultures.
- Vultures as vectors of anthrax disease: A simple mechanistic model.

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