Combining radio-telemetry and radar measurements to test optimal foraging in an aerial insectivore bird

Itai Bloch[1]*, David Troupin[1], Sivan Toledo[2], Ran Nathan[3] and Nir Sapir[1]

[1]Department of Evolutionary and Environmental Biology and Institute of Evolution, University of Haifa, Haifa, Israel
[2]Blavatnik School of Computer Science, Tel-Aviv University, Israel
[3]Department of Ecology, Evolution, and Behaviour, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Israel

* Correspondence to: itaibloch2@gmail.com

SUMMARY

Optimal foraging theory posits that foragers adjust their movements based on prey abundance to optimize food intake. While extensively studied in terrestrial and marine environments, aerial foraging has remained relatively unexplored due to technological limitations. This study, uniquely combining BirdScan-MR1 radar and the ATLAS biotelemetry system, investigates the foraging dynamics of Little Swifts (*Apus affinis*) in response to insect movements over Israel's Hula Valley. Insect Movement Traffic Rate (MoTR) substantially varied across days, strongly influencing swift movement. On days with high MoTR, swifts exhibited reduced flight distance, increased colony visit rate, and earlier arrivals at the breeding colony, reflecting a dynamic response to prey availability. However, no significant effects were observed in total foraging duration, flight speed, or daily route length. Notably, as insect abundance increased, inter-individual distances decreased. These findings suggest that Little Swifts optimize their foraging behavior in relation to aerial insect abundance, likely influencing reproductive success and population dynamics. The integration of radar technology and biotelemetry systems provides a unique perspective on the interactions between aerial insectivores and their prey, contributing to a comprehensive understanding of optimal foraging strategies in diverse environments.

Keywords

aeroecology, ATLAS biotelemetry system, central-place foraging, Hula Valley, Little Swift, movement ecology, predator-prey interactions, radar entomology

INTRODUCTION

Optimal foraging theory predicts how foragers should adjust their movement and behavior based on the costs and benefits of finding and consuming food [1–5]. Empirical studies have tested optimal foraging predictions in terrestrial and marine environments [6–10], yet, to the best of our knowledge, no study has thus far utilized advanced tracking tools to empirically examine optimal foraging predictions of foragers in the highly dynamic aerial habitat [11]. Understanding optimal foraging in aerial habitats is essential for comprehending complex interactions and adaptations in this dynamic environment. We combine aerial insect abundance data collected using the BirdScan-MR1 radar [12–15] with measurements of the movement of insectivore birds using the automated and accurate ATLAS (Advanced Tracking and Localization of Animals in Real-Life Systems) biotelemetry system [16]. This study examines whether the Little Swift (*Apus affinis*), a monomorphic, small insectivore (12 cm, 25 g) that breeds in small colonies and often forages in groups [17–20], optimizes its foraging behavior in response to variations in insect density in the airspace, within the framework of optimal central-place foraging. We note that in a preliminary study, we found no discernible differences in foraging characteristics between males and females [21].

Aerial insectivores feed on insects [22–24] that have recently been reported to be in decline in different ecosystems and regions of the world [22,23,25–27]. Among aerial foragers, swifts are highly adapted to life on the wing due to their high flight capabilities, allowing them to undertake different activities in the air and stay airborne for long periods [28–34]. Nevertheless, during the breeding season, birds return to their central-place breeding colony and provide food to their young throughout the day. Consequently, they may adjust their foraging in relation to different environmental conditions to maximize the net energy obtained during foraging [4,35,36]. According to the theory of central-place foraging, traveling to a distant destination is an expensive investment in terms of time and energy compared to traveling to a nearby destination [37,38]. Therefore, animals are expected to prefer reducing the time and distance of travel to the food patch and thus will travel farther only when their prey is not sufficiently available near the central place. We thus hypothesize that, in times of abundant food, birds will optimize energy conservation by foraging closer to the colony [37,39]. Consequently, we anticipate a reduction in both the average daily air flight distance (hereafter – average distance) (Prediction 1) and the maximum daily air flight distance (hereafter – maximum distance) (Prediction 2) from the breeding colony under conditions of increased food abundance. This will also result in shorter overall daily flight route length (hereafter - daily route) (Prediction 3) and overall daily foraging flight duration (hereafter – foraging duration) (Prediction 4). Since breeding swifts may maximize food provisioning to the young, the visitation rate could also be tailored to the abundance of insects [2,3,37] such that higher food density will facilitate a higher rate of visits at the nest [2,6] (Prediction 5). Furthermore, a bird's flight speed, when feeding its young, is expected to vary with food abundance, and this rarely tested prediction suggests an increase in flight speed with greater food abundance [40,41] (Prediction 6). The timing of morning emergence from the colony and evening return to the colony is affected by a number of factors [42–47]. These include predation risks that vary throughout the daily cycle and the optimization of foraging time in relation to food abundance. We hypothesize that the time of arrival at the colony for the night roost and the time of departure from the colony in the morning will be affected by the abundance of flying insects. We specifically predict that swifts will arrive at the colony earlier for roosting when food abundance is sufficiently high to provide enough food for their own and their young’s needs (Prediction 7). If insect abundance is correlated in time such that birds may be able to predict insect abundance based on that of the previous day, We expect the swifts' departure time to be delayed when the abundance of insects on the previous day is higher (Prediction 8), as there is no need to maximize the foraging duration if food is abundant and this could reduce predation risk by avian predators that are active early in the morning [48,49]. Consequently, the predicted swifts' emergence times are expected to correlate with the roosting time from the previous night (Prediction 9a). Yet, if no between-day correlation in insect abundance exists, morning departure timing will not be related to insect abundance of the previous day and the two measures will not be correlated. (Prediction 9b). For social foraging animals, local enhancement can provide several advantages, including increased energy intake [50–52], higher fitness [53], improved food detection [54,55], and avoidance of predators [53,56]. However, an enlarged group size could exacerbate inter-individual competition and may lead to diminished foraging efficiency [53,57]. Conversely, increased food abundance ensures adequate sustenance for more group members, thereby alleviating competition. We posit that higher insect abundance would lead to a greater density of foraging individuals, reducing the distance between them during foraging. (Prediction 10).

To test these predictions, we studied how Little Swifts adjust their aerial foraging behavior to varying insect abundances in the airspace. Using radar and biotelemetry data, we reveal bird response to food abundance in relation to foraging distances, timing, foraging duration, and speed, as well as the frequency of colony visits and the distance between individuals. Our findings shed light on how aerial foragers may optimize their movement and behavior in response to highly dynamic environmental conditions.

RESULTS

The MoTR (1207.7 ± 566.7 insects km^{-1} hr^{-1}) varied substantially between different days during the swifts' breeding season, with a minimum of 164.4 and a maximum of 2518.9 insects km^{-1} hr^{-1} (n=31 days; Fig 1a). No seasonal trend was found in MoTR (Spearman's rank correlation between the ordinal date and the MoTR, ρ=-0.007, p=0.971, n=31 days; Table 1). We found a significant negative effect of the MoTR on the swifts' average distance from the breeding colony (Prediction 1) (estimate<-0.001, t=-5.27, p<0.001, n=31 days, Gamma GLM; Fig 1b). Similarly, a significant negative effect of MoTR was also found in relation to the birds' maximum distance from the breeding colony (Prediction 2) (estimate=-1.818, t=-3.52, p=0.001, n=31 days, Gaussian GLM; Fig 1c). We found no effect of MoTR on the daily route (Prediction 3) (estimate<-0.001, t=-1.65, p=0.123, n=15 days, Gamma GLM) and on the duration of foraging (Prediction 4) (estimate=0.029, t=1.05, p=0.315, n=15 days, Gaussian GLM). The frequency of visits at the breeding colony (Prediction 5) (see the average model in Table 2) was significantly and positively affected by MoTR (estimate=0.001, t=3.78, p<0.001, n=31 days, Gamma GLM; Fig 1d) and negatively affected by the distance of the birds from the breeding colony (estimate<-

0.001, t=2.03, p=0.043, n=31 days). We found that there was no effect of MoTR on the average flight speed (Prediction 6) (estimate<-0.001, t=-1.33, p=0.193, n=31 days, Gaussian GLM). The time of arrival at the breeding colony for nighttime roosting was significantly and negatively affected by the MoTR (Prediction 7) (estimate=-0.011, t=-2.27, p=0.034, n=23 days, Gaussian GLM), such that birds arrived earlier to roost in days characterized by abundant insect prey. The departure time from the breeding colony following overnight roosting has resulted in a consistently observed duration of nighttime roosting (10.45 ± 0.68 hours). This duration showed no correlation with the preceding day's MoTR (Prediction 8) (estimate=0.002, t=0.26, p=0.801, n=20, Gaussian GLM). Conversely, it was significantly and positively influenced by the evening arrival time to the colony on the prior day (Prediction 9a) (estimate=0.634, t=2.81, p=0.016, n=14 days, Gaussian GLM; Fig 1e). Furthermore, the departure time from the roost exhibited no association with MoTR of the same day (Prediction 9b) (estimate=-0.005, t=-1.07, p=0.297, n=20, Gaussian GLM). MoTR significantly and negatively affected (estimate<-0.001, t=-3.12, p=0.004, n=31 days, Gamma GLM) the distance between individuals (Prediction 10), while, as expected, the distance between individuals was significantly and positively correlated with the distance from the colony (estimate<0.001, t=5.02, p<0.001, n=31 days; Fig 1f).

Table 1 - Summary of the statistical analyses.

Dependent Variable	Independent Variable	Estimate	t-value	p-value	Sample Size	Statistical Test
Seasonal trend: Average Daily MoTR	Ordinal Date	-0.007		0.971	31 days	Spearman's Rank Correlation
Pred. 1: Average Distance from Breeding Colony	Average Daily MoTR	<-0.001	-5.27	<0.001	31 days	Gamma GLM
Pred. 2: Maximum Distance from Breeding Colony	Average Daily MoTR	-1.818	-3.52	0.001	31 days	Gaussian GLM

<u>Pred. 3:</u> Daily route	Average Daily MoTR	<-0.001	-1.65	0.123	15 days	Gamma GLM
<u>Pred. 4:</u> Daily Duration of Foraging	Average Daily MoTR	0.029	1.05	0.315	15 days	Gaussian GLM
<u>Pred. 5:</u> Frequency of Visits at Breeding Colony	Average Daily MoTR (The first of two independent variables)	0.001	3.78	<0.001	31 days	Gamma GLM
	Distance from Breeding Colony (The second of two independent variables)	<-0.001	2.03	0.043	31 days	
<u>Pred. 6:</u> Average Flight Speed	Average Daily MoTR	<-0.001	-1.33	0.193	31 days	Gaussian GLM
<u>Pred. 7:</u> Evening Arrival Time to Breeding Colony	Average Daily MoTR	-0.011	-2.27	0.034	23 days	Gaussian GLM
<u>Pred. 8:</u> Departure from Breeding Colony (overnight stay)	MoTR on the Previous Day	0.002	0.26	0.801	20 days	Gaussian GLM
<u>Pred. 9a:</u> Departure from Breeding Colony (overnight stay)	Evening Arrival Time to Breeding Colony (previous day)	0.634	2.81	0.016	14 days	Gaussian GLM
<u>Pred. 9b:</u> Departure from Breeding Colony (overnight stay)	MoTR on the Same Day	-0.005	-1.07	0.297	20 days	Gaussian GLM
<u>Pred. 10:</u> Distance between Individuals	Average Daily MoTR (The first of two independent variables)	<-0.001	-3.12	0.004	31 days	Gamma GLM
	Distance from Breeding Colony (The second of two independent variables)	<0.001	5.02	<0.001	31 days	

Table 2 - Top models (ΔAIC < 2) for colony visit frequency. The best model includes "Distance from Breeding Colony" and "Average Daily MoTR."

Model	Intercept	Distance from Breeding Colony	Average Daily MoTR	df	LogLik	AICc	Delta	Weight
4	2.174	<-0.001	0.001	4	-108.2	225.9	0.00	0.626
3	1.093		0.001	3	-110.1	227.1	1.13	0.356

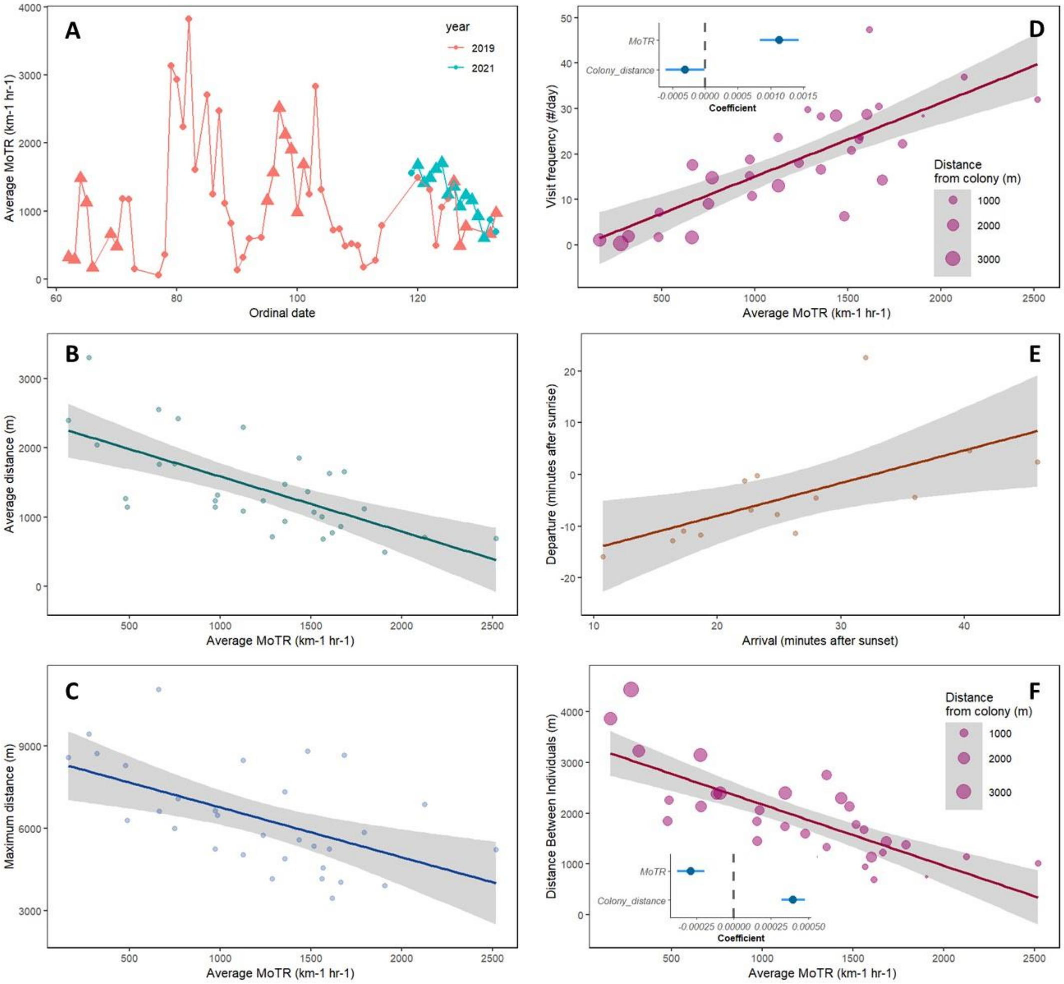


Fig 1. Insect Traffic Rate (MoTR) and its effects on the aerial foraging of Little Swifts. **A -** Average daily insect abundance in relation to an ordinal date. Triangles represent days when data allowed examining swift movement in relation to MoTR. MoTR varied across days within the swifts' breeding season by more than an order of magnitude. **B -** The effect of MoTR on the average flight distance from the breeding colony. **C -** The effect of MoTR on the maximal flight distance from the breeding colony. **D -** The effect of MoTR on the average daily frequency of visits at the breeding colony; inset: coefficient value and confidence intervals of the coefficient resulting from the model testing the effects of MoTR and distance from the breeding colony on the frequency of visits. **E -** The relationship between the time of departure from the breeding colony in the morning after the overnight stay and the time of arrival to the colony prior to the overnight stay the previous evening. **F -** The effect of MoTR on the daily average distance between foraging individuals; inset: coefficient value and confidence intervals of the coefficient

resulting from the model testing the effects of MoTR and distance from the colony on the distance between individuals.

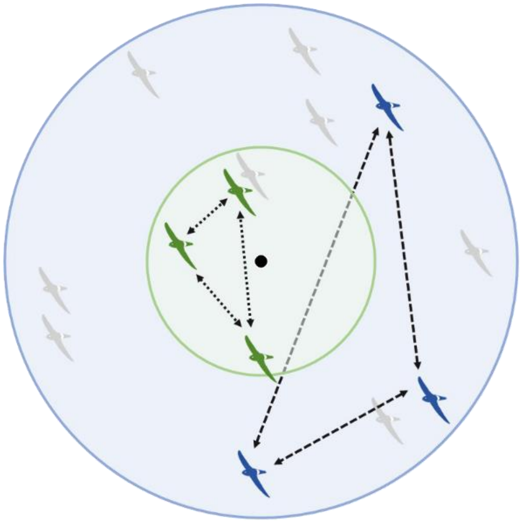


Fig 1 - Figure Supplement 1 - An expected increase in the average distance between individuals with an increase in the distance from the breeding colony (black circle in the center of the figure).

DISCUSSION

Movement optimization during breeding

Our study provides novel insights regarding the optimal foraging of aerial insectivores, by uniquely employing advanced tools to simultaneously track the movement and behavior of insectivore foragers and the dynamics of their insect prey aloft. We observed a reduction in average and maximum flight distance (Prediction 1 & 2) from the breeding colony in relation to MoTR, indicating that swifts can identify insect prey abundance and accordingly modify their flight distance and avoid using distant foraging locations when sufficient prey is found near the breeding colony. These results indicate that a significant decrease in insect abundance may lead swifts to expend more energy foraging in distant areas from the breeding colony, potentially impacting parental flight efficiency. Providing food to the young is a critical and enduring activity in bird life, influencing physiology [58,59], immunity [60], and survival [59,61]. Consequently, a reduction in flying insect abundance forcing birds to forage farther from the colony could have broad implications for the reproduction, survival, and population ecology of insectivores. Nevertheless, we investigated the impact of MoTR on the total daily route and foraging duration (Prediction 3 & 4). Our findings revealed no significant effects, suggesting that daily energy expenditure attributed to flight behavior does not exhibit a consistent pattern in response to the highly variable insect prey abundance and the associated shifts in swift flight behavior (higher proximity to the colony when prey is abundant).

While the theory of central-place foraging suggests that traveling to a distant destination is an expensive investment in terms of time and energy utilization compared to traveling to a nearby destination [37–39], our findings indicate that the birds may optimize their feeding rate (Prediction 5) to the young by staying close to the colony when food is abundant. We found that the frequency of colony visits was positively affected by MoTR (Fig 1e), indicating high provisioning rates when food was abundant, which supports an increase in the overall energy brought to the nestlings [62]. Thus, even when the birds foraged close to the colony under optimal conditions, the shorter traveling distance did not necessarily confer lower flight-related energetic expenditure because more return trips were made. Rather, it is the ability to provide more food to the young, by foraging close to the colony, that is being optimized, to benefit the reproductive output of the birds.

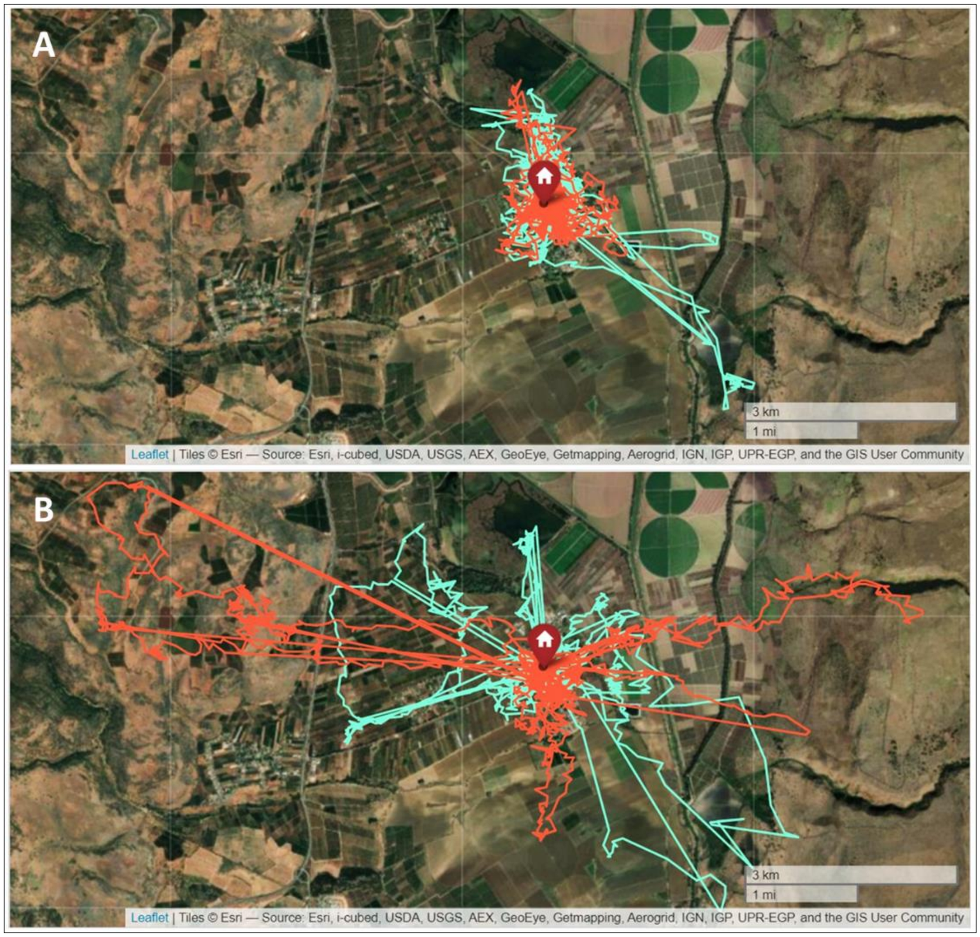
The availability of resources in a bird's habitat may affect the length of its daily route [63], while others show no significant correlation [64]. We found that the swifts maintained rather constant flight effort, regardless of the abundance of their prey. Similarly, foraging duration was also not related to MoTR. Further, our results suggest that food abundance had no significant impact on flight speed (Prediction 6). Consequently, our results support the idea that birds optimize food provisioning to the young during breeding, which could increase the birds' reproductive success at the expense of foraging energetics considerations. Another property of food provisioning to the young that may affect energy intake is the size of the load but unfortunately, we have no information on whether the load size brought to the nest varied with insect abundance.

Behavior optimization during breeding

Birds may adjust their foraging timing to optimize food intake [42–45]. Our findings reveal that when insect prey was abundant in the airspace, the swifts' evening arrival time (Prediction 7) at the breeding colony was earlier than in days when insects were scarce. This result aligns with prior research on the predation risk-food availability trade-off, indicating that birds tend to avoid foraging during twilight hours due to elevated predation risk during this period[43,65].

The availability of insects did not significantly influence the departure time (Prediction 8) from the colony after an overnight stay on both the same and previous days. Yet, the morning departure time was positively and significantly correlated with the time of arrival at the overnight roosting on the previous day. This result suggests a link between these specific behavioral features related to roosting timing. A possible explanation could be that birds arriving at the colony relatively early in the evening may be hungrier the following day, and this hunger may cause an earlier departure for foraging the following morning (Prediction 9a). Also, since these birds fed their young earlier, they may prefer to start foraging earlier the following morning, and thereby provide more food to their young in the morning to compensate for the early termination of feeding on the previous day (Prediction 9b). Further research is needed to establish the causes of this interesting relationship.

The influence of resource abundance on social foraging in aerial insectivorous birds remains a largely unexplored topic, despite its potential impact on bird fitness [53], energy intake [50,53,57], predator avoidance [53,56], and food acquisition dynamics [54,55]. Our findings suggest that when food is abundant, the distance between foraging individuals (Prediction 10) is reduced, and this distance increases when food is scarce. A possible explanation for these findings is that when individuals forage at an increasing distance from the breeding colony (Fig 2) they may be too far from each other to detect each other and forage together in patchily distributed insect-rich patches in the airspace. When foraging closer to each other, local enhancement of individuals may take place when an effective foraging area is discovered [52,66]. Thus, swifts likely benefit from the advantages of local enhancement during periods of abundant food [50–52], but this enhancement might be limited when food is scarce.



Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

Fig 2. **Foraging range in relation to insect abundance.** Differences in the movement routes of two individuals (marked in light blue and orange) on two consecutive days that were characterized by large differences in MoTR. **A** – 09.04.2019 (average MoTR=1904.2 insects km^{-1} hr^{-1}). **B** – 10.04.2019 (average MoTR=983.5 insects km^{-1} hr^{-1}).

Central-place foraging

Many studies on central-place foraging examined foraging characteristics in relation to the distance and quality of the foraging patch [10,35,38,39,67–70]. Our research deals with the abundance of food in the aerial habitat, which is highly dynamic, as corroborated by our findings that insect abundance varied greatly, by more than an order of magnitude, between different days during the swifts' breeding period. Although insect abundance aloft varies with time, it is not clear to what extent it varies in space as several studies suggested that insect bioflow is correlated over large spatial scales [71–73]. Hence, patches of high insect concentration might be transient and spatially variable; thus, further study is needed to characterize the spatial properties of insect bioflow. It is known that insect concentrations occur under specific meteorological conditions, for example on the edges of air fronts [74], as well as near topographic features where the wind may subside [75]. We call for a better description of the spatial properties of insects in the aerial habitat, specifically the horizontal and vertical distribution of insects in the airspace and how it might be affected by different factors, including topography, coastlines and weather conditions. Our study, with its primary focus elsewhere, did not delve into this aspect. Nonetheless, the availability of today's advanced technological tools attests to the feasibility of conducting such research.

Integrating advanced tracking systems for ecological research

Due to its nature, aeroecological research is limited by the paucity of appropriate tools to track aerial animals and their dynamic environment in detail [76,77]. Several recent technological developments facilitated a better grasp of the aerial environment, allowing the examination of various aspects of aerial ecology that were impossible to test in the past or that were explored only with coarse resolution[78]. The combination of two advanced systems, namely ATLAS and the BirdScan-MR1 radar allows, for the first time, a detailed investigation of fundamental aspects of animal foraging in the airspace through the study of predator-prey interactions between Little Swifts and their insect prey. Recent progress in wildlife tracking technologies enables new insights into the movement patterns of animals, including their causes, consequences, and underlying mechanisms, facilitated by the integration of complementary tools [79], as demonstrated here. Specifically, the unique combination of advanced technologies to expand the boundaries of aeroecological research can be expanded and further utilized for understanding how changes in the aerial habitat that are related to human activities may affect organisms that live in this unique and dynamic habitat [22,23]. These insights may play a crucial role in the conservation of aerial insectivores that are dramatically affected by human related alteration, including habitat degredation and the use of pesticides [80,81].

METHODS

Little Swifts breed in Israel between March and September, during which they complete two breeding cycles. In the swifts' breeding colony, dozens of pairs inhabit interconnected nests crafted from feathers and stems. Each nest features a narrow entrance designed to deter predators and obscure visibility inside. This setup presents challenges in accurately assessing nesting conditions and determining the age of chicks within the nests. Both partners incubate alternately, and during the night, they both stay in the nest. The incubation period lasts 18-22 days, and fledging occurs 35-40 days after hatching. Both parents participate in the feeding of the young [18,19]. We studied swifts in a breeding colony located in the center of the Hula Valley in northeastern Israel (33.05°N / 35.59°E). The valley consists of a mosaic of agricultural land with various crops, mainly deciduous tree plantations and open field crops, as well as wetlands and urbanized areas. Our field observations suggest that there are about 30-40 nesting pairs in the colony.

Swift movement data collection

During March-May of 2019 and 2021, employing a 9 m mist net outside the breeding colony, we captured Little Swifts during their early morning departure after the night stay. Our bird trapping activities were conducted under permits (2019-42174 and 2021-42762) of the Israel Nature and Parks Authority. Captured swifts were measured and ringed with a standard aluminum ring to allow individual identification. We equipped 32 swifts with ATLAS transmitters weighing 1-1.15 g, less than 5% of the body mass of each individual.

The ATLAS system is a reverse GPS-like system that operates using time-difference-of-arrival of radio waves to base stations (antennas), recording the horizontal locations of tagged animals within the system's coverage area at high frequency (the tags transmitted every 8 s) and spatial accuracy (~ 10 m). The system includes antennas deployed throughout the Hula Valley and the surrounding area (Fig 3), facilitating the calculation of the spatial position of the radio transmitters that emit a unique ID signal for each transmitter. The transmitters were affixed to the swifts using a backpack harness positioned between the back feathers, secured with Perma-Type Surgical Cement (Perma-Type Company Inc., Plainville, CT, USA). This adhesive naturally dries and allows the harness to fall off after several weeks [82]. Except for one tag that stopped transmitting immediately after release, the tags operated for periods of 0.3 - 39.8 days (X=13.4 ±10.4 days).

We analyzed a total of 841,342 localizations during days in which we obtained both bird movement data from the ATLAS system and insect abundance data from the radar (see below). The data were collected over a total of 31 days (19 days in 2019 and 12 days in 2021). Because swifts are active during the daytime, we used only ATLAS data from the main activity hours of the swifts during the day, from sunrise to sunset [83] (personal observations and movement data obtained from the ATLAS system).

We applied several filters to reduce inaccuracies in the movement tracks as a result of localization errors [84]. Since there is no accurate information about the maximum flight speed of Little Swifts, we relied on the maximum flight speed of the Common Swift [32] to filter out tracks with a flight speed that exceeded 30 m/s (9.6% of the raw data). We additionally utilized the standard error of the localization (StdLoc) to assess position quality, identifying outliers (1.5 times the interquartile range) of StdLoc [85]. Setting an upper limit at 30.1 m, we filtered out positions with low accuracy, amounting to 10.7% of the data. Additionally, we applied a minimum threshold of 4 [86] for the Number of ATLAS Base Stations (NBS) receiving a tag's signals during each transmission to filter out localizations with low confidence of accuracy (4.0% of the data; range of NBS after filtering: 4-14, $\bar{X}$=6.6 ±1.9 NBS). We then excluded tracks in which consecutive locations were more than 500 m away from each other (0.7% of the data), likely representing an error in the automatic calculation of the tag’s position. The filtering process removed a total of 24.5% of the raw data. To ensure the overall dataset represented the movement of all birds without being influenced by the unusual behavior of a few, we excluded data from days with fewer than four active tags (range of number of tags after filtering: 4-10, mean±SD = 6.9±1.5 tags per day). This threshold eliminated days with a small number of tagged birds recorded (24.8% of the data). As a result, a total of 49.4% of the original raw data was excluded to maintain a high level of reliability and accuracy; analysis was based on 415,420 positions, with a mean of 1,491 ± 899 locations per tag per day.

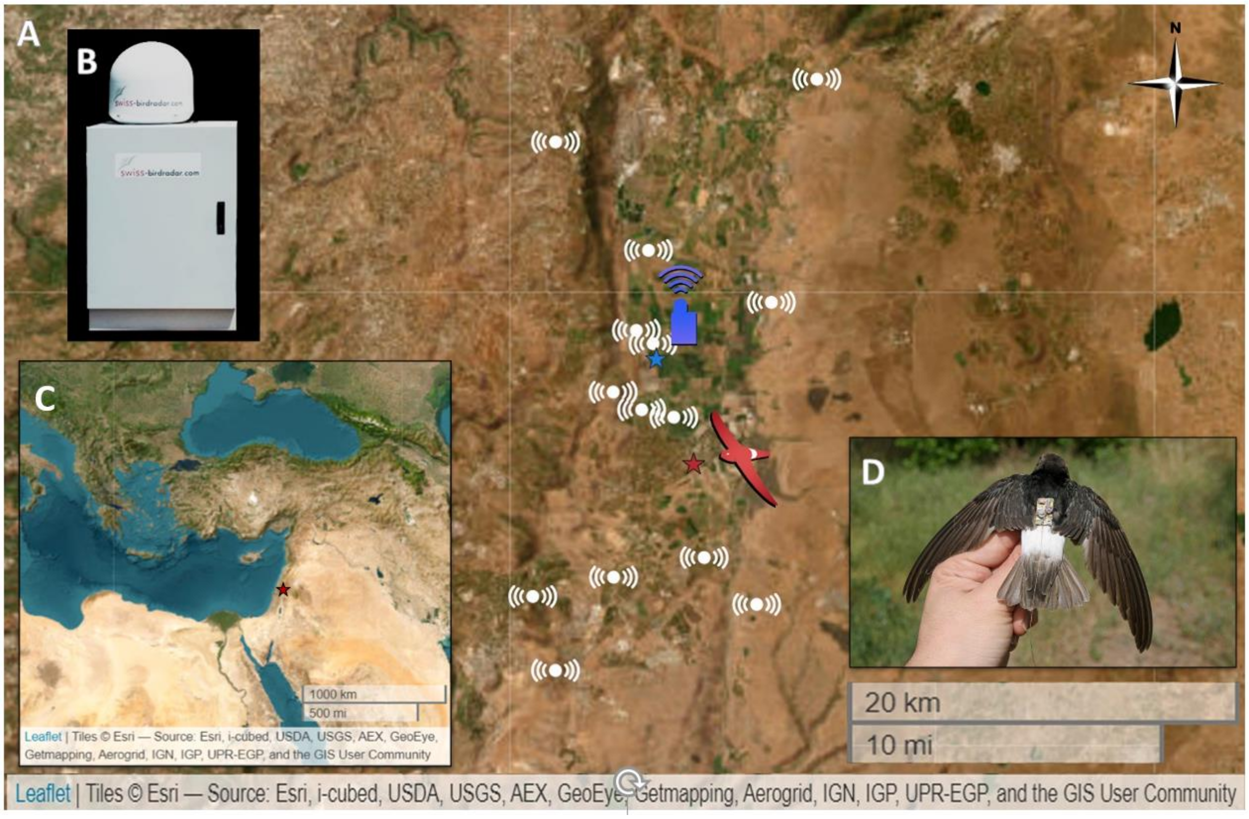


Fig 3. **The research system**. **A** - Map of the Hula Valley, Israel, and the surrounding area. The red star represents the location of the Little Swifts' breeding colony. The blue star depicts the location of the radar. White markings indicate the locations of the ATLAS system's antennas. **B** – The BirdScan-MR1 radar. **C** - The location of the research system in northeastern Israel within the Middle East, is indicated by a red star. **D** - A Little Swift with an ATLAS tag.

Movement analysis

To examine bird movement (Fig 2) and behavior, we calculated the average and maximum distance from the breeding colony. To determine the average daily route and duration of foraging, we analyzed data from 15 days with a minimum of 10 hours of consistent tag activity, excluding cases of tag malfunction or battery issues. There was no tag reception when the swifts entered the building that housed their breeding colony, allowing easy determination of when they visited the colony. To standertize the effect of day length on the foraging duration, we calculated and subtracted the day length from the total daily foraging time (Day duration - Daily foraging duration = Net foraging duration). The resulting data represent the foraging duration in relation to sunrise and sunset, independent of day length. To characterize the rate of visitation to the breeding colony, we defined visits as events in which birds stayed in the colony for at least 60 seconds. The time of arrival to the breeding colony for night roosting was calculated as minutes after sunset, within a 60-minute window around sunset, and the same was done for the morning departure time, but in relation to sunrise. We calculated the average departure and arrival time of all active tags for each day.

We omitted days when the night time arrival to the colony was missing (e.g., days when the battery ran out during the day) or days when the morning departure time from the colony was missing. Consequently, we were left with 23 days of arrival data, 20 days of departure data, and 20 days of departure in which data existed regarding the abundance of insects (below) on the previous day. To compute the average distance between individuals, we calculated the average position every 5 min for each bird and omitted cases where we had simultaneous location data of less than 4 individuals. We then calculated the daily average of the distance between individuals.

Radar measurements of insect abundance

Studies have shown that environmental variables like temperature and wind significantly influence the spatial abundance of insects across different crop areas [73,87]. To estimate the abundance of insects aloft, we used the daily average MoTR of aerial insects recorded by the BirdScan-MR1 radar [15] (Swiss-birdradar, Winterthur, Switzerland) located in the Hula Valley (33.06°N / 35.35°E), 6.5 km north of the Little Swifts' breeding colony. The radar is capable of detecting flying animals, including songbirds, waterbirds, bird flocks, large single birds, and insects, by classifying them according to the patterns of the echo [12,88]. The Radar Cross Section (RCS) quantifies the reflectivity of a target, serving as a proxy for size by representing the crosssectional area of a sphere with identical reflectivity to water, whose diameter equals the target's body length [89]. Recent findings indicate that the BirdScan MR1 radar can detect insects with an RCS as low as 3 mm² [90], with decreasing detection probability at increasing altitudes. The detection threshold, defined by the STC setting, was 93 dBm, and the transmit power was 25 kW [90]. These capabilities make the radar suitable for locating the primary prey of swifts, which typically range in size from 1 to 16 mm [17]. In addition, the radar automatically calculates the height, speed, and direction of movement of the object. The radar has an upward-pointing antenna that picks up objects passing within a 90-120° vertical cone over it. Insects are recorded by the radar from a height of about 50 m above ground level up to a height of about 700 m above the ground. We calculated the daily averaged MoTR from 5 am to 8 pm local time as a standard measure of insect abundance rates. This was done by counting insects per hour across a 1 km cross-section and averaging these counts over a single day, allowing for comparisons of aerial movement between different days [13]. We matched the insect data obtained from the radar with the swift movement data obtained from the ATLAS system.

Statistical analysis

Using the 'stats' package in R [91], we applied Generalized Linear Models (GLMs) and Spearman correlations to explore the effects of the MoTR (continuous independent variable) on the movement and behavior parameters of the swifts during the breeding season. If the GLM, with more than one explanatory variable, had a ΔAIC<2 relative to other models, we employed the MuMIn [92] package to generate an average model. Specifically, we investigated how the distance between individuals is influenced by both the distance of birds from the colony and MoTR. Accounting for the expected increase in individual distance when flying farther from the breeding colony due to a larger air volume occupied by the moving birds, these factors were integrated into our GLM analysis. The same approach was applied in modeling the frequency of visits to the colony. To distinguish the effects of breeding colony distance and insect abundance on the distance between individuals, our GLM incorporated both variables, ensuring a comprehensive understanding of the impact of distance from the colony (Fig 1 - Figure

Supplement 1). In the model testing which factors affected the time of arrival at the colony, the frequency of visits was highly correlated with MoTR and was therefore removed from the model at an initial stage. The departure time from the colony and the length of the daily route did not significantly affect the arrival time and were left out of the model at a later stage. Consequently, the final model included only MoTR as an explanatory factor for colony arrival time. We additionally tested if the time of departure from the breeding colony after the overnight stay was related to three explanatory variables, MoTR, MoTR on the previous day, and the arrival time to the colony for the overnight stay on the previous day. We used the fitdistrplus package [93] to identify the appropriate distribution for each GLM. We used R (version 4.1.2, R Development Core Team) [91] for all the statistical analyses. Data reported are average ± S.D. unless noted otherwise and the analyses were two-tailed with a critical $\alpha=0.05$.

Declaration of interests

The authors declare no competing interests.

Acknowledgments

We thank Yosef Kiat, Eve Miller, Ayla Rimon, Stav Shay, and Gev Galili for their help with the fieldwork and Yoni Vortman, Yoav Bartan, Yotam Orchan, and Anat Levi for logistical support.

Funding

The study was supported by a grant from the KKL-JNF (Kanfei KKL, contract no. 60-05-675-18) and the Israel Science Foundation grants ISF-2333/17 and ISF-1653/22 (to N.S.), ISF-965/15 (to R.N. and S.T), and ISF-1919/19 (to S.T). The ATLAS system work was funded by the Minerva Foundation, the Minerva Center for Movement Ecology, the Adelina and Massimo Della Pergola Professor of Life Sciences to R.N.

REFERENCES

1. Pyke GH, Pulliam HR, Charnov EL. Optimal foraging: A selective review of theory and tests. The Quarterly Review of Biology. 1977;52(2):137–154. doi:10.1086/409852
2. Pyke GH. Optimal foraging theory: A critical review. Annual Review of Ecology and Systematics. 1984;15(1):523–575. doi:10.1146/annurev.es.15.110184.002515
3. Schoener TW. Theory of feeding strategies. Annual Review of Ecology and Systematics. 1971;2(1):369–404. doi:10.1146/annurev.es.02.110171.002101
4. Emlen JM. The role of time and energy in food preference. The American Naturalist. 1966;100(916):611–617. doi:10.1086/282455
5. MacArthur RH, Pianka ER. On optimal use of a patchy environment. The American Naturalist. 1966;100(916):603–609. doi:10.1086/282454
6. Kramer DL, Nowell W. Central place foraging in the Eastern Chipmunk, *Tamias striatus*. Animal Behaviour. 1980;28(3):772–778. doi:10.1016/S0003-3472(80)80137-0
7. Crowder LB. Optimal foraging and feeding mode shifts in fishes. Environmental Biology of Fishes. 1985;12(1):57–62. doi:10.1007/BF00007710
8. Lincoln AE, Quinn TP. Optimal foraging or surplus killing: Selective consumption and discarding of salmon by brown bears. Behavioral Ecology. 2019;30(1):202–212. doi:10.1093/beheco/ary139
9. Staniland IJ, Gales N, Warren NL, Robinson SL, Goldsworthy SD, Casper RM. Geographical variation in the behaviour of a central place forager: Antarctic fur seals. Marine Biology. 2010;157(11):2383–2396. doi:10.1007/S00227-010-1503-8
10. Holder K, Polis GA. Optimal and central-place foraging theory applied to a desert harvester ant, *Pogonomyrmex californicus*. Oecologia. 1987;72(3):440–448. doi:10.1007/BF00377577

11. Diehl RH. The airspace is habitat. Trends in Ecology and Evolution. 2013;28(7):377–379. doi:10.1016/j.tree.2013.02.015

12. Zaugg S, Saporta G, Van Loon E, Schmaljohann H, Liechti F. Automatic identification of bird targets with radar via patterns produced by wing flapping. Journal of The Royal Society Interface. 2008;5(26):1041–1053. doi:10.1098/RSIF.2007.1349

13. Liechti F, Aschwanden J, Blew J, Boos M, Brabant R, Dokter AM, Kosarev V, Lukach M, Maruri M, Reyniers M, et al. Cross-calibration of different radar systems for monitoring nocturnal bird migration across Europe and the Near East. Ecography. 2019;42(5):887–898. doi:10.1111/ecog.04041

14. Nilsson C, Dokter AM, Schmid B, Scacco M, Verlinden L, Bäckman J, Haase G, Dell'Omo G, Chapman JW, Leijnse H, et al. Field validation of radar systems for monitoring bird migration. Journal of Applied Ecology. 2018;55(6):2552–2564. doi:10.1111/1365-2664.13174

15. Knop E, Grimm ML, Korner-Nievergelt F, Schmid B, Liechti F. Patterns of high-flying insect abundance are shaped by landscape type and abiotic conditions. Scientific Reports. 2023;13(1):1–8. doi:10.1038/s41598-023-42212-z

16. Toledo S, Shohami D, Schiffner I, Lourie E, Orchan Y, Bartan Y, Nathan R. Cognitive map-based navigation in wild bats revealed by a new high-throughput tracking system. Science. 2020;369(6500):188–193. doi:10.1126/science.aax6904

17. Collins CT, Anderson MD, Johnson DN. Food of the Little Swift *Apus affinis* and African Black Swift *Apus barbatus* in South Africa. Ostrich. 2010;81(1):45–50. doi:10.2989/00306525.2010.455818

18. Shirihai H, Dovrat E, Christie DA, Harris A. The Birds of Israel. London: Academic Press; 1996.

19. Paz U. The birds of Israel. Stephen Greene Press; 1987.

20. del Hoyo J, Elliott A, Sargatal J, Christie D., Kirwan G. Common Swift (*Apus apus*). In: Del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E, editors. Handbook of the Birds of the World Alive. Barcelona: Lynx Edicions; 2020.

21. Bloch I, Troupin D, Sapir N. Movement and parental care characteristics during the nesting season of the Little Swift (Apus affinis) [Poster presentation]. 12th European Ornithologists' Union Congress. Cluj Napoca, Romania. 2019.

22. Hallmann CA, Foppen RPB, Van Turnhout CAM, De Kroon H, Jongejans E. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature. 2014;511(7509):341–343. doi:10.1038/nature13531

23. Møller AP. Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. Ecology and Evolution. 2019;9(11):6581–6587. doi:10.1002/ece3.5236

24. Bowler DE, Heldbjerg H, Fox AD, de Jong M, Böhning-Gaese K. Long-term declines of European insectivorous bird populations and potential causes. Conservation Biology. 2019;33(5):1120–1130. doi:10.1111/cobi.13307

25. Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, et al. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE. 2017;12(10):e0185809. doi:10.1371/journal.pone.0185809

26. Wagner DL. Insect declines in the anthropocene. Annual Review of Entomology. 2020;65:457–480.

27. Benton TG, Bryant DM, Cole L, Crick HQP. Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology. 2002;39(4):673–687. doi:10.1046/j.1365-2664.2002.00745.x

28. Rattenborg NC. Do birds sleep in flight? Naturwissenschaften. 2006;93(9):413–425. doi:10.1007/s00114-006-0120-3

29. Sachs G. Energy saving of aerial roosting swifts by dynamic flap-gliding flight. Journal of Ornithology. 2017;158(4):943–953. doi:10.1007/s10336-017-1447-6

30. Hedenström A, Norevik G, Warfvinge K, Andersson A, Bäckman J, Åkesson S. Annual 10-month aerial life phase in the Common Swift *Apus apus*. Current Biology. 2016;26(22):3066–3070. doi:10.1016/j.cub.2016.09.014

31. Bäckman J, Alerstam T, Backman J, Alerstam T. Confronting the winds: orientation and flight behaviour of roosting swifts, *Apus apus*. Proceedings of the Royal Society B: Biological Sciences.

2001;268(1471):1081–1087. doi:10.1098/rspb.2001.1622

32. Henningsson P, Johansson LC, Hedenström A. How swift are swifts *Apus apus*? Journal of Avian Biology. 2010;41(1):94–98. doi:10.1111/j.1600-048X.2009.04850.x

33. Hedrick TL, Pichot C, de Margerie E. Gliding for a free lunch: biomechanics of foraging flight in Common Swifts (Apus apus). The Journal of Experimental Biology. 2018;221(22):jeb186270. doi:10.1242/jeb.186270

34. Liechti F, Witvliet W, Weber R, Bächler E. First evidence of a 200-day non-stop flight in a bird. Nature Communications. 2013;4(1):1–7. doi:10.1038/ncomms3554

35. Charnov EL. Optimal foraging, the marginal value theorem. Theoretical Population Biology. 1976;9(2):129–136. doi:10.1016/0040-5809(76)90040-X

36. Pianka ER. Natural selection of optimal reproductive tactics. American Zoologist. 1976;16(4):775–784. doi:10.1093/icb/16.4.775

37. Orians GH, Pearson NE. On the ecology of central place foraging Horn DJ, Stairs GR, Mitchelle R., editors. Analysis of ecological systems. 1979:155–177.

38. Bell WJ. Central place foraging. In: Searching behaviour: The behavioural ecology of finding resources. Dordrecht: Springer Netherlands; 1990. p. 171–187. doi:10.1007/978-94-011-3098-1_12

39. Olsson O, Brown JS, Helf KL. A guide to central place effects in foraging. Theoretical Population Biology. 2008;74(1):22–33. doi:10.1016/j.tpb.2008.04.005

40. Norberg RA. Optimal flight speed in birds when feeding young. The Journal of Animal Ecology. 1981;50(2):473. doi:10.2307/4068

41. Hedenstrom A, Alerstam T. Optimal flight speed of birds. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences. 1995;348(1326):471–487. doi:10.1098/RSTB.1995.0082

42. Bednekoff PA, Houston AI. Avian daily foraging patterns: Effects of digestive constraints and variability. Evolutionary Ecology 1994 8:1. 1994;8(1):36–52. doi:10.1007/BF01237664

43. Bonter DN, Zuckerberg B, Sedgwick CW, Hochachka WM. Daily foraging patterns in free-living birds: exploring the predation–starvation trade-off. Proceedings of the Royal Society B: Biological Sciences. 2013;280(1760). doi:10.1098/RSPB.2012.3087

44. Amichai E, Kronfeld-Schor N. Artificial light at night promotes activity throughout the night in nesting Common Swifts (*Apus apus*). Scientific reports. 2019;9(1):1–8. doi:10.1038/s41598-019-47544-3

45. Salamolard M, Weimerskirch H. Relationship between foraging effort and energy requirement throughout the breeding season in the Wandering Albatross. Functional Ecology. 1993;7(6):643. doi:10.2307/2390184

46. Harding AMA, Piatt JF, Schmutz JA, Shultz MT, Van Pelt TI, Kettle AB, Speckman SG. Prey density and the behavioral flexibility of a marine predator: the Common Murre (*Uria aalge*). Ecology. 2007;88(8):2024–2033. doi:10.1890/06-1695.1

47. Metcalfe NB, Ure SE. Diurnal variation in flight performance and hence potential predation risk in small birds. Proceedings of the Royal Society B: Biological Sciences. 1995;261(1362):395–400. doi:10.1098/RSPB.1995.0165

48. Lang SDJ, Mann RP, Farine DR. Temporal activity patterns of predators and prey across broad geographic scales. Behavioral Ecology. 2019;30(1):172–180. doi:10.1093/beheco/ary133

49. Roth TC, Lima SL. The predatory behavior of wintering Accipiter hawks: Temporal patterns in activity of predators and prey. Oecologia. 2007;152(1):169–178. doi:10.1007/S00442-006-0638-2

50. Brown CR. Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators. Animal Behaviour. 1988;36(3):780–792. doi:10.1016/S0003-3472(88)80161-1

51. Flemming SP, Smith PC, Seymour NR, Bancroft RP. Ospreys use local enhancement and flock foraging to locate prey. Auk. 1992;109(3):649–654.

52. Krebs JR. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour. 1974;51(1–2):99–131. doi:10.1163/156853974x00165

53. Giraldeau L-A, Caraco T. Social foraging theory. Princeton University Press; 2000. doi:10.1515/9780691188348/PDF

54. Cvikel N, Egert Berg K, Levin E, Hurme E, Borissov I, Boonman A, Amichai E, Yovel Y. Bats aggregate to improve prey search but might be impaired when their density becomes too high. Current Biology. 2015;25(2):206–211. doi:10.1016/J.CUB.2014.11.010

55. Bijleveld AI, van Gils JA, Jouta J, Piersma T. Benefits of foraging in small groups: An experimental study on public information use in Red Knots *Calidris canutus*. Behavioural Processes. 2015;117:74–81. doi:10.1016/J.BEPROC.2014.09.003

56. Sorato E, Gullett PR, Griffith SC, Russell AF. Effects of predation risk on foraging behaviour and group size: Adaptations in a social cooperative species. Animal Behaviour. 2012;84(4):823–834. doi:10.1016/j.anbehav.2012.07.003

57. Beauchamp G. The effect of group size on mean food intake rate in birds. Biological Reviews. 1998;73(4):449–472. doi:10.1111/j.1469-185X.1998.tb00179.x

58. Karell P, Pietiäinen H, Siitari H, Pihlaja T, Kontiainen P, Brommer JE. Parental allocation of additional food to own health and offspring growth in a variable environment. Canadian Journal of Zoology. 2009;87(1):8–19. doi:10.1139/Z08-133

59. Bukaciński D, Bukacińska M, Spaans AL. Experimental evidence for the relationship between food supply, parental effort and chick survival in the Lesser Black-backed Gull Larus fuscus. Ibis. 1998;140(3):422–430. doi:10.1111/j.1474-919x.1998.tb04603.x

60. Appleby BM, Anwar MA, Petty SJ. Short-term and long-term effects of food supply on parasite burdens in Tawny Owls, *Strix aluco*. Functional Ecology. 1999;13(3):315–321. doi:10.1046/J.1365-2435.1999.00319.X

61. Brinkhof MWG, Cave AJ. Food supply and seasonal variation in breeding success: an experiment in the European Coot. Proceedings of the Royal Society of London. Series B: Biological Sciences. 1997;264(1380):291–296. doi:10.1098/RSPB.1997.0041

62. McCarty JP. The number of visits to the nest by parents is an accurate measure of food delivered to nestlings in Tree Swallows. Journal of Field Ornithology. 2002:9–12. doi:10.1648/0273-8570-73.1.9

63. Stauss MJ, Burkhardt JF, Stauss JT, And Tomiuk JF, Stauss MJ, Burkhardt JF, Tomiuk J. Foraging flight distances as a measure of parental effort in Blue Tits *Parus caeruleus* differ with environmental conditions. Journal of Avian Biology. 2005;36(1):47–56. doi:10.1111/J.0908-8857.2005.02855.X

64. Tremblay I, Thomas D, Blondel J, Perret P, Lanbrechts MM. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. Ibis. 2005;147(1):17–24. doi:10.1111/J.1474-919X.2004.00312.X

65. Lima SL. Initiation and termination of daily feeding in Dark-eyed Juncos: Influences of predation risk and energy reserves. Oikos. 1988;53(1):3. doi:10.2307/3565656

66. Harel R, Spiegel O, Getz WM, Nathan R. Social foraging and individual consistency in following behaviour: Testing the information centre hypothesis in free-ranging vultures. Proceedings of the Royal Society B: Biological Sciences. 2017;284(1852). doi:10.1098/rspb.2016.2654

67. Bryant DM, Turner AK. Central place foraging by swallows (Hirundinidae): The question of load size. Animal Behaviour. 1982;30(3):845–856. doi:10.1016/S0003-3472(82)80158-9

68. Kacelnik A, Cuthill I. Central place foraging in starlings (*Sturnus vulgaris*). II. Food allocation to chicks. The Journal of Animal Ecology. 1990;59(2):655. doi:10.2307/4887

69. Rosenberg DK, McKelvey KS. Estimation of habitat selection for central-place foraging animals. The Journal of Wildlife Management. 1999;63(3):1028. doi:10.2307/3802818

70. Elgin AS, Clark RG, Morrissey CA. Tree Swallow selection for wetlands in agricultural landscapes predicted by central-place foraging theory. The Condor. 2020;122(4):1–12. doi:10.1093/condor/duaa039

71. Chapman JW, Reynolds DR, Smith AD, Riley JR, Pedgley DE, Woiwod IP. High-altitude migration of the Diamondback Moth *Plutella xylostella* to the U.K.: a study using radar, aerial netting, and ground trapping. Ecological Entomology. 2002;27(6):641–650. doi:10.1046/J.1365-2311.2002.00472.X

72. Welti EAR, Zajicek P, Frenzel M, Ayasse M, Bornholdt T, Buse J, Classen A, Dziock F, Engelmann RA, Englmeier J, et al. Temperature drives variation in flying insect biomass across a German malaise trap network. Insect Conservation and Diversity. 2022;15(2):168–180. doi:10.1111/icad.12555

73. Goulson D, Derwent LC, Hanley ME, Dunn DW, Abolins SR. Predicting calyptrate fly populations

from the weather, and probable consequences of climate change. Journal of Applied Ecology. 2005;42(5):795–804. doi:10.1111/J.1365-2664.2005.01078.X

74. Reynolds DR, Chapman JW, Drake VA. Riders on the wind: The aeroecology of insect migrants. In: Aeroecology. Springer International Publishing; 2018. p. 145–178. doi:10.1007/978-3-319-68576-2_7

75. Drake VA, Reynolds DR. Insect migratory flight II: Concentrations and disturbances. In: Radar entomology: observing insect flight and migration. Wallingford UK: CABI; 2012. p. 254–281. doi:10.1079/9781845935566.0254

76. Nathan R. Long-distance dispersal research: Building a network of yellow brick roads. Diversity and Distributions. 2005;11(2):125–130. doi:10.1111/j.1366-9516.2005.00159.x

77. Kunz TH, Gauthreaux SA, Hristov NI, Horn JW, Jones G, Kalko EKV, Larkin RP, McCracken GF, Swartz SM, Srygley RB, et al. Aeroecology: probing and modeling the aerosphere. Integrative and Comparative Biology. 2008;48(1):1–11. doi:10.1093/ICB/ICN037

78. Nathan R, Sapir N, Trakhtenbrot A, Katul GG, Bohrer G, Otte M, Avissar R, Soons MB, Horn HS, Wikelski M, et al. Long-distance biological transport processes through the air: can nature's complexity be unfolded in silico? Diversity and Distributions. 2005;11(2):131–137. doi:10.1111/J.1366-9516.2005.00146.X

79. Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, Assaf M, Baktoft H, Beardsworth CE, Bertram MG, Bijleveld AI, et al. Big-data approaches lead to an increased understanding of the ecology of animal movement. Science. 2022;375(6582). doi:10.1126/science.abg1780

80. Stanton RL, Morrissey CA, Clark RG. Tree swallow (*Tachycineta bicolor*) foraging responses to agricultural land use and abundance of insect prey. Canadian Journal of Zoology. 2016;94(9):637–642. doi:10.1139/cjz-2015-0238

81. Nocera JJ, Blais JM, Beresford D V., Finity LK, Grooms C, Kimpe LE, Kyser K, Michelutti N, Reudink MW, Smol JP. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous chimney swifts. Proceedings of the Royal Society B: Biological Sciences. 2012;279(1740):3114–3120. doi:10.1098/rspb.2012.0445

82. Johnson G, Pebworth J, Ornithology HK-J of F, 1991 U. Retention of transmitters attached to passerines using a glue-on technique (Retención de transmisores en Passeriformes utilizando la técnica de pegamentos). Journal of Field Ornithology. 1991;62(4):486–491.

83. Thieurmel B, Elmarhraoui A. suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.5.0. 2019.

84. Gupte PR, Beardsworth CE, Spiegel O, Lourie E, Toledo S, Nathan R, Bijleveld AI. A guide to pre-processing high-throughput animal tracking data. Journal of Animal Ecology. 2022;91(2):287–307. doi:10.1111/1365-2656.13610

85. Tukey JW. Exploratory data analysis. London: Addison-Wesley; 1977.

86. Arnon E, Cain S, Uzan A, Nathan R, Spiegel O, Toledo S. Robust Time-of-Arrival Location Estimation Algorithms for Wildlife Tracking. Sensors. 2023;23(23). doi:10.3390/s23239460

87. Grüebler MU, Morand M, Naef-Daenzer B. A predictive model of the density of airborne insects in agricultural environments. Agriculture, Ecosystems and Environment. 2008;123(1–3):75–80. doi:10.1016/j.agee.2007.05.001

88. Zaugg S, Schmid B, Liechti F. Ensemble approach for automated classification of radar echoes into functional bird sub-types. In: Radar Aeroecology. 2017. p. 1. doi:10.13140/RG.2.2.23354.80326

89. Chilson PB, Stepanian PM, Kelly JF. Radar aeroecology. Aeroecology. 2018 Mar 23:277–309. doi:10.1007/978-3-319-68576-2_12/FIGURES/10

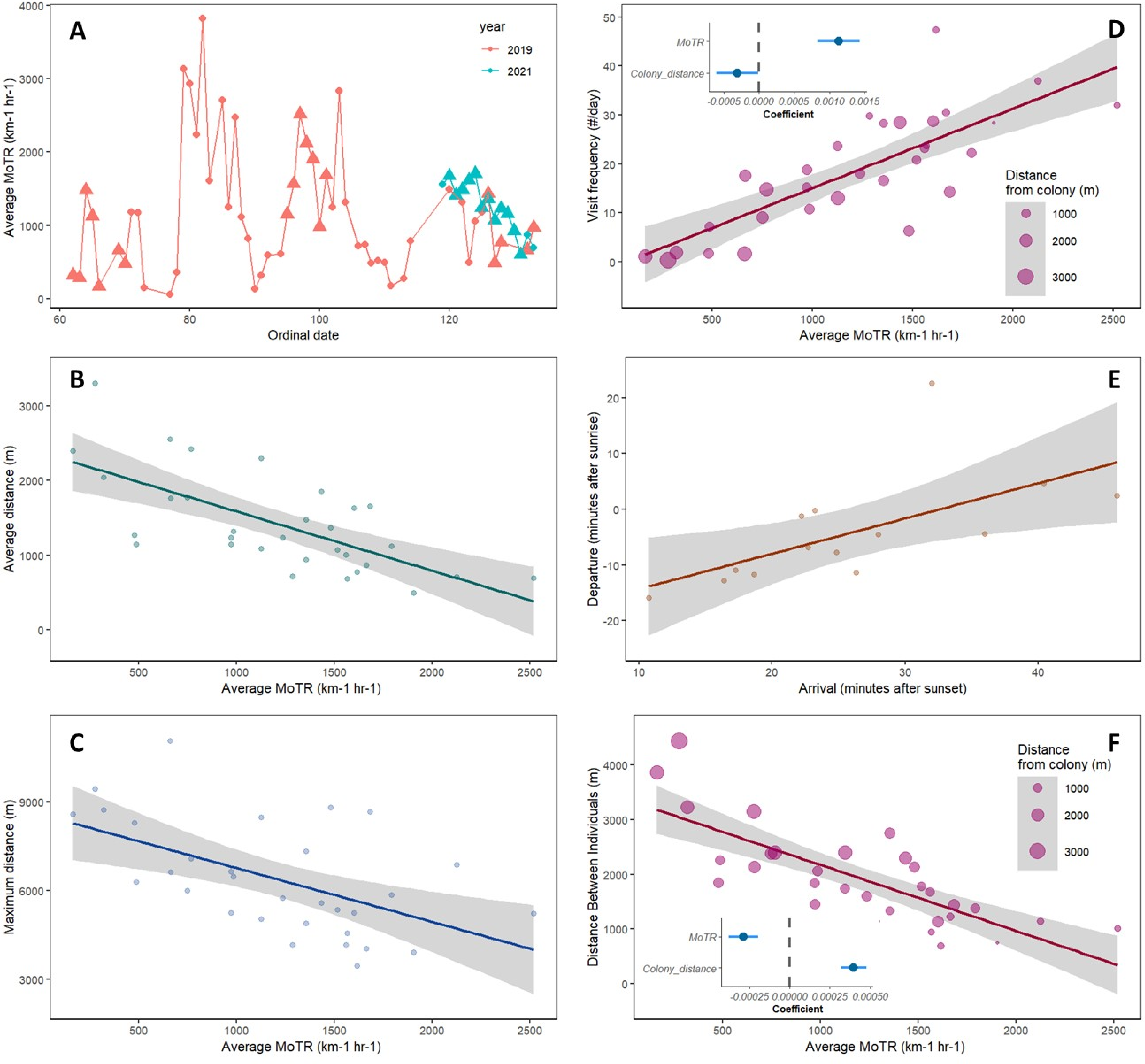
90. Haest B, Liechti F, Hawkes WL, Chapman J, Åkesson S, Shamoun-Baranes J, Nesterova AP, Comor V, Preatoni D, Bauer S. Continental-scale patterns in diel flight timing of high-altitude migratory insects. 2024. doi:10.1098/rstb.2023.0116

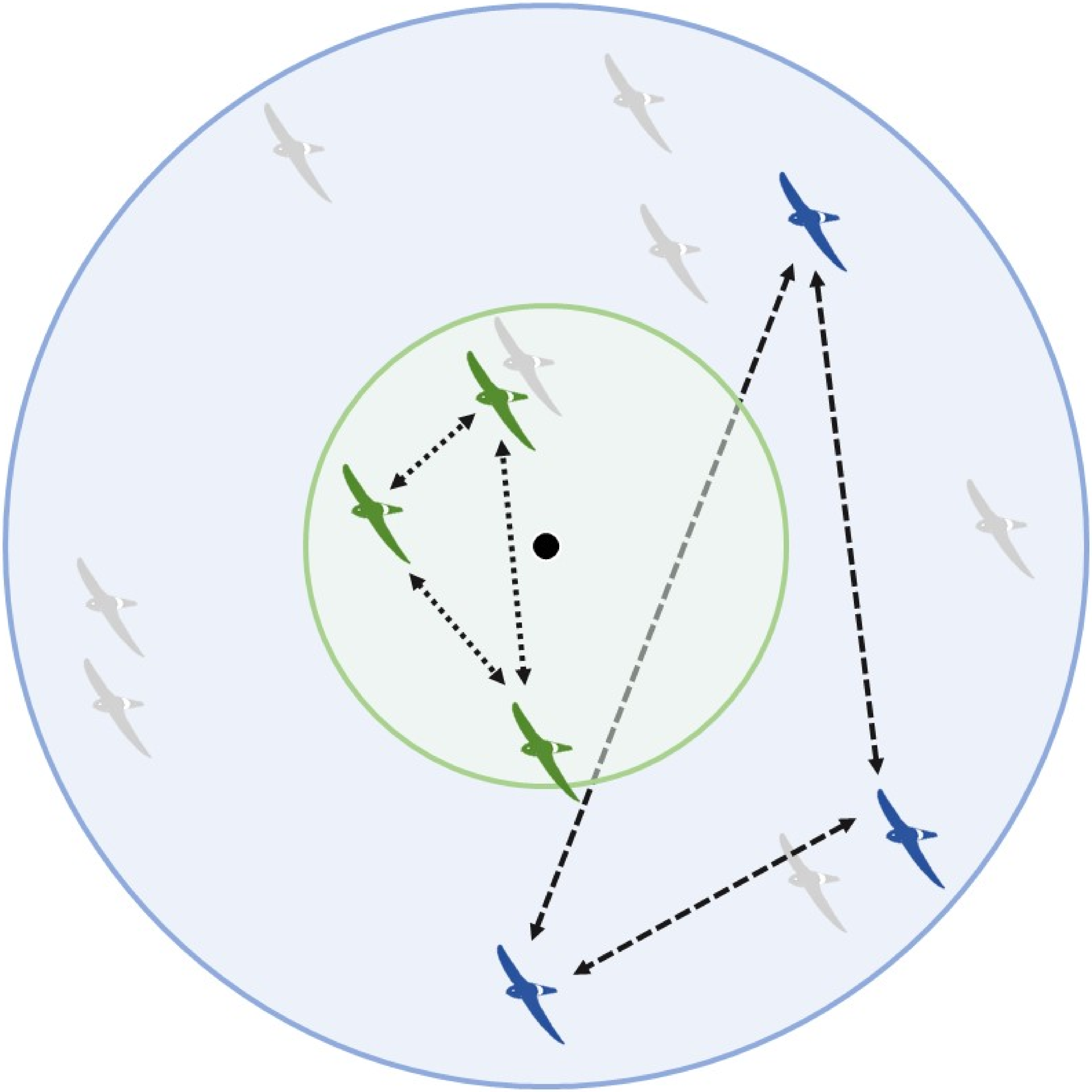
91. Team RC. R: A language and environment for statistical computing. 2021.

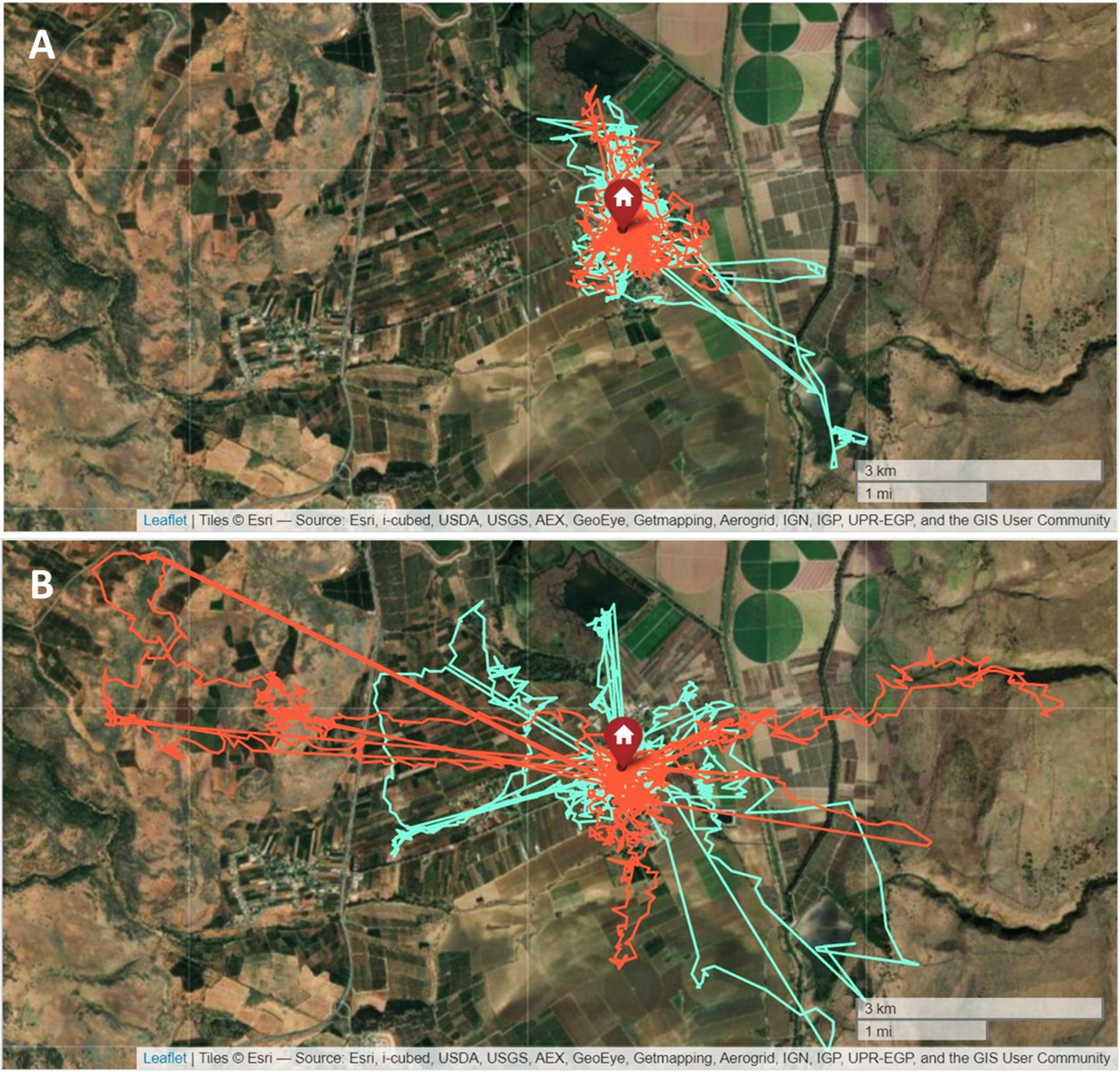
92. Barton K. MuMIn: Multi-Model Inference. R package version 1.43.17. 2021.

93. Delignette-Muller ML, Dutang C. fitdistrplus: An R package for fitting distributions. Journal of

Statistical Software. 2015;64(4):1–34. doi:10.18637/JSS.V064.I04


A
year
2019
2021
Average MoTR (km-1 hr-1)
Ordinal date
B
Average distance (m)
Average MoTR (km-1 hr-1)
C
Maximum distance (m)
Average MoTR (km-1 hr-1)
D
MoTR
Colony_distance
Coefficient
Visit frequency (#/day)
Distance from colony (m)
1000
2000
3000
Average MoTR (km-1 hr-1)
E
Departure (minutes after sunrise)
Arrival (minutes after sunset)
F
Distance from colony (m)
1000
2000
3000
Distance Between Individuals (m)
MoTR
Colony_distance
Coefficient
Average MoTR (km-1 hr-1)




A
3 km
1 mi
Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community
B
3 km
1 mi
Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community


A
B
swiss-birdradar.com
swiss-birdradar.com
N
C
1000 km
500 mi
Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community
D
20 km
10 mi
Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community