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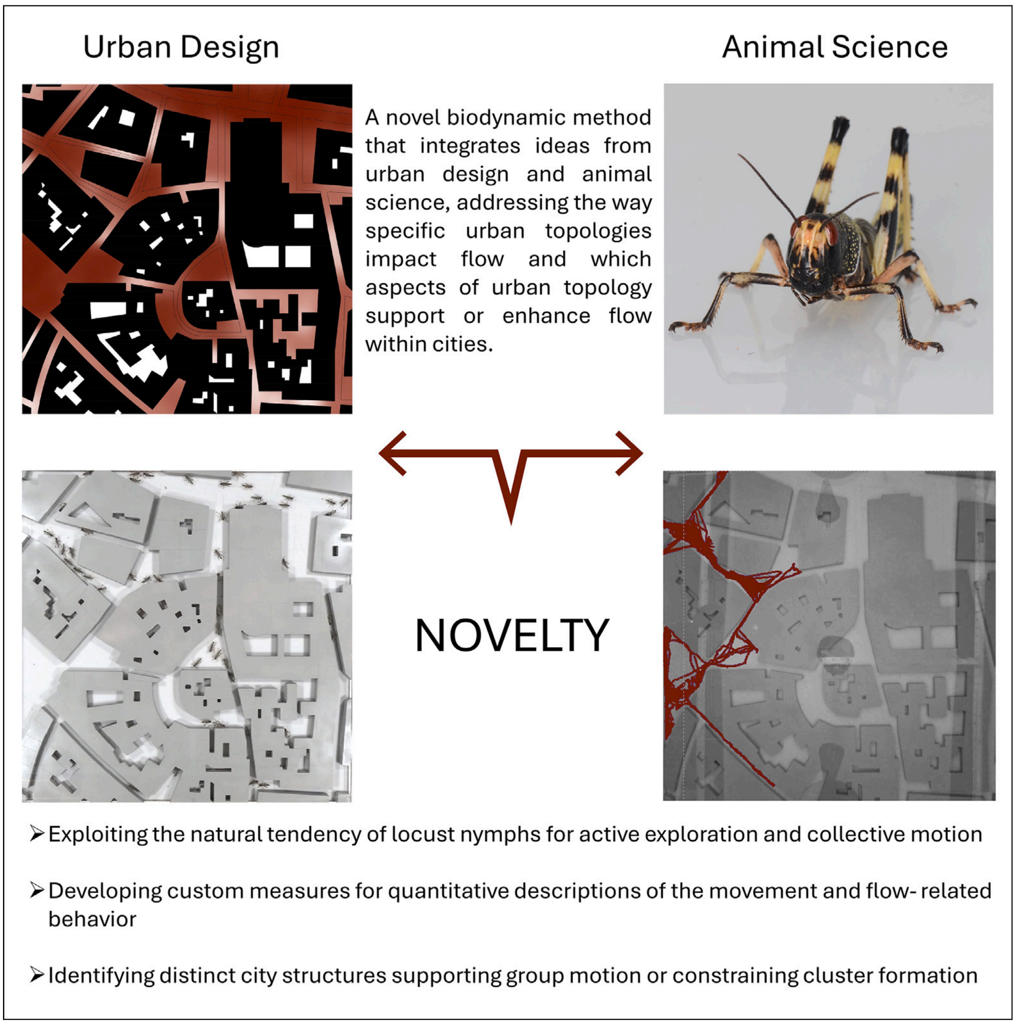

Moshe Guershon, Roee Mordechai Francos, Amir Ayali, Tali Hatuka

ayali@post.tau.ac.il

Highlights

The interaction between urban topology and flow is instrumental for the city's life

The comparative analysis of flow in cities is challenging but essential

In this study we combine urban design and animal science for dynamic flow research

The use of living insects and physical city models allow novel unexpected insights

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Locust behavior and city topology: A biodynamic approach for assessing urban flows

Moshe Guershon,[1,2,6] Roee Mordechai Francos,[3,6] Amir Ayali,[1,4,7,*] and Tali Hatuka[5]

SUMMARY

A city's economic growth and the inhabitants' wellbeing are highly affected by its topology and connecting networks, which, in turn, influence movement and flows in the city. Flow relates to how a city is developed, organized, managed, and built. The analysis of flow in cities is challenging but essential. In this study, the fields of urban design and animal science are combined, and a new approach for exploring the relationships between urban topology and physical flow is developed. Specifically, we establish an interdisciplinary methodology to evaluate mobility performance in various urban settings, utilizing experimental observations of the dynamic behavior of natural-biological agents, i.e., locusts, within physical city models. Our novel approach enriches the currently available toolbox by using living organisms as indicators for flow in physical city models. Our findings improve our understanding of the intricate flow interactions in urban settings.

INTRODUCTION

Since the initial development of urban environments, flow has been one of the core factors influencing how cities function and develop. This flow includes people, machines, and materials. "Cities exist through the networks that create them, and the development of these networks is contingent on the characteristics of the urban space".[1] Furthermore, these networks impact the city's economic growth and the wellbeing of its inhabitants. However, flow is not only an economic or technical concept; it also has social and spatial components related to how cities develop and how cities are organized, managed and built. In recent decades, the formalization of the "space of flows" concept[2] has contributed to the diversity of flows in contemporary cities.[1] Conceptually, flow is an elastic concept, and its definition varies in different locations and throughout history. The analysis of flow in cities involves both contextual and temporal considerations and is thus challenging but essential, as it contributes to maintaining social order and effectively managing cities and operation processes. Furthermore, understanding flow is fundamental for planning and developing cities. More recently, flow and urban networks have become a focus of attention due to three interrelated changes affecting contemporary cities: (1) densification and rapid urban growth, which impose heavy loads on existing infrastructures[3]; (2) digitization and economic competition, which increase the need for efficiency[4,5]; and (3) climate change and the need to develop compact cities.[6] These factors have led to increased research on flow, as the efficient functioning of a city's transportation and communication systems are essential for its economic growth and synchronized flow contributes to the development of more livable, resilient, and sustainable cities. In short, flow involves multiple processes and factors and can also be perceived as a solution for multiple challenges, such as the development of new spatial systems that can track the increasingly wide repercussions of the population location, employment and related spatial interactions.[7]

There are two distinct but prominent approaches for examining flow.[8] The first approach involves typo-morphological analysis, which is based on descriptive and deductive methods.[9] This approach can be used to answer questions related to the evolution, rhythms, and walkability of cities and urban areas. However, this approach is inadequate for addressing questions related to performance[10] and/or the complexity of a city's diffuse urban forms.[11] These limitations have led to the development of another approach, which is based on complex theory and quantitative methods.[12] This approach uses computer simulations and models to investigate how changes in city structure might impact the flow of simulated agents (simulated pedestrian flow, traffic, etc.)[13,14] Recently, there have been efforts to integrate the two approaches, combining urban design analysis with statistical clustering methods.[15] On the basis of these ongoing efforts to better understand city flows and develop new exploratory methods, in our multidisciplinary study, we propose a method that integrates ideas from urban design and animal science, addressing how specific urban topologies impact flow and what aspects of urban topology support or enhance flow within cities.

[1]School of Zoology, Tel Aviv University, Tel Aviv, Israel
[2]The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel
[3]Faculty of Computer Science, Technion—Israel Institute of Technology, Haifa, Israel
[4]Sagol School of Neuroscience, Tel Aviv University, Tel Aviv, Israel
[5]Porter School of the Environment and Earth Sciences, Tel Aviv University, Tel Aviv, Israel
[6]These authors contributed equally
[7]Lead contact
*Correspondence: ayali@post.tau.ac.il
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Urban topology refers to the city's physical structure and morphology, which often shape flow and influence movement.[16] A city's distinct spatial prototype is based on a design approach with similar elements, such as street networks, building forms, and open spaces, reflecting the city topology. Although city topologies may differ, cities are often classified by their typology. Burke et al.[15] suggested the following classification of urban typologies: "small world, monumental, radial, garden, linear, atomized, random, organic, grid, and fractal"; this classification allows comparisons and generalization among different cities. Flow, including aggregations and collective motion, is a ubiquitous phenomenon in many natural systems, from large herds of herbivores to bird flocks, fish schools, and insect swarms. Important aspects of the self-emergence of collective animal motion models include interactions between individuals, interactions among the group, and interactions with the physical environment. Spatial structures can facilitate or impede the development and maintenance of collective motion. Clearly, despite urban design and animal science differences, social and spatial aspects influence the dynamics and management of flow and aggregation in both fields. Moreover, agency is a key factor affecting the flow dynamics in both fields that often cannot be predicted by computer simulations.

The underlying hypothesis of our study is that particular city types have distinct effects on mobility performance in urban environments. Exploring this hypothesis will contribute to enhancing flow in existing cities and the development of future cities. Following this rationale, we developed an innovative methodological approach based on three anchors: typo-morphological analysis (urban design), network and graph theory analysis (computation), and animal behavior analysis (biology). In developing this approach, we chose three cases that do not represent a comprehensive study of topologies but are used as tools to provide insights into the analysis and methodological approach. Accordingly, our study included three phases. (1) The construction of physical city models: we built scaled-down, physical models of three cities, New York, Cairo, and Rome. Each city has a distinct network topology (New York, reticular; Rome, hierarchical; and Cairo, Poisson). Each city's topology represents a distinct type of urban typology (e.g., grid, monumental, and organic). (2) Experiments: we exploited the natural tendency of desert locust nymphs (nonflying, juvenile stage) to swarm. Locusts are a quintessential example of natural collective motion.[17] Their behavior includes strong attraction to conspecifics and aggregation, as well as synchronized coordinated motion. These characteristic behavioral traits are known to be robust and persist even in the presence of topographical constraints.[18] We utilized state-of-the-art computer video analysis techniques to track the movement of individual locusts, monitor the interactions between the insects within the different city topologies and monitor the interaction of the insects' group motion with the specific city layout. (3) Analysis: information about the movement of individual locusts and the collective motion of the group was extracted from the data. The parameters calculated at the individual locust level included the walking speed, distance covered, walking bout duration, and pause durations. At the group level, we calculated the mean distance between locusts, mean cluster size, order parameter, and other parameters. To analyze the experimental results, we developed *LocusTracker*, a computer vision software tool consisting of reliable, accurate, video-based visual trackers to determine and predict the locust trajectories. This software enables an improved understanding of locust movement patterns by enabling researchers to track individual locusts in urban environment models over long periods (several hours) without needing physical markers on individual locusts. With this methodology, we performed a novel biodynamic study on the functional interactions between urban topology and flow.

Our novel biodynamic approach for assessing urban topology and flow enriches the currently available toolbox with experimental observations of natural-biological agents' dynamic behavior within physical city models. Furthermore, we focus on both microlevel aspects of city structure and generic patterns of urban typologies. The use of living organisms as indicators or surrogates for certain aspects of flow in urban typology provides new insights for the future development of cities, focusing on human and nonhuman movements (i.e., crowd dynamics, transportation and mobility dynamics, and autonomous vehicles). To our knowledge, this is the first time this approach has been envisioned or presented.

RESULTS

The use of biological agents as tools for exploring city typologies

In developing the methodology to evaluate how different city topologies impact flow, we focused on three distinct city typologies (Figure 1A): grid, monumental, and organic. For each typology, we chose a representative city, each with a different active area, road width and length, and number and distribution of corners. Figure S1 details the particular features of the studied areas.

The biological agents utilized for the study were last instar desert locust nymphs (Figures 1B and 1C), which are known for their tendency to aggregate and migrate in dense swarms, referred to as marching bands.[17] A group of 50 locusts were introduced into each city model via an arbitrarily chosen entrance point and allowed to move freely through the city streets and open spaces for 3 h, enabling uninterrupted interactions with both other insects and the wooden city model (Figure 1D). The overall kinematics of the individual locust movements were consistent with those previously described for locusts in commonly used laboratory experimental arenas and natural settings.[19,20] Our LocusTracker algorithm allowed continuous monitoring of individual locusts and the group of locusts throughout the experiments, indicating that the locusts demonstrated typical pause-and-go kinematic motions,[17,19] which are characterized by walking bouts separated by pauses of different durations (Table S1). These motions were largely independent of interactions with the specific intra- and intercity topology.

Locust behavior and walking trajectories in the various topologies

We closely explored the individual locomotion behavior and walking trajectories, and the results showed that the locusts demonstrated variable individual patterns, as well as coordinated (small) group movements (see Video S1). The different individual trajectories likely reflected the individual insect states and their specific interactions with both the group and the city topology (Figure 2; Table S1). While some locusts explored most of the available space, "roaming the streets" of the model (Figure 2A), other locusts limited their exploration to a section of the

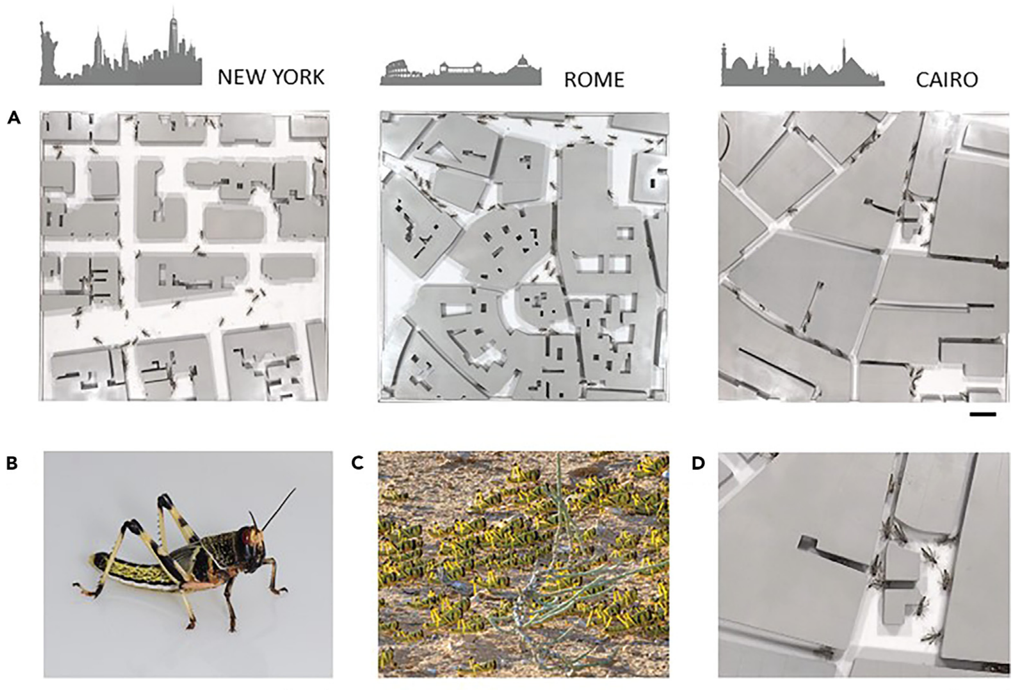

Figure 1. Locusts in the city—the experiments

(A) Experiments—tracking the movements and flow of 50 locusts in three different city models: New York City, Rome, and Cairo.

(B) A desert locust last instar nymph.

(C) Locusts demonstrating collective motion in natural settings.

(D) A group of locusts interacting with distinct city topologies. Scale bars 10 cm in A and D; 1 cm in B.

city area or to specific spaces within the city model (Figures 2B and 2C, respectively). Although the three examples in Figure 2 are from the three different city models, this does not intend to suggest clear correlations between specific type of locomotion behaviors and specific city models.

In addition to tracking the walking trajectories of the individual insects, we constructed heatmaps (see details in the STAR methods section) to understand the cumulative occupancy of insects in different parts of the city models. Heatmaps were generated for three nonoverlapping 30 min segments for each of the three city models (Figure 3). The analysis results reveal that the locusts tend to explore the entire available space; however, the locusts also show preference for specific regions within the city models, including wider streets (e.g., Figure 3A, New York, top panel) and city squares (e.g., Figure 3C, Cairo, bottom panel).

Locusts' preferences and distinct features of city topologies

Next, to elucidate the interactions among the insects and the city environment, we divided the available space in each model into four categories based on the street (or open space) width (from 1 = widest, to 4 = narrowest; Figure S1; see details in the STAR methods section). Figure 4 describes the distribution of the locusts among the different street categories in each of the city models. As shown in Figure 4A, while each city model has its own unique division into the four street categories, the overall trend is similar among the models: categories 1 and 2 include the majority of the available space, with category 2 including ~40–50% of the space. A comparison of the actual distribution of the locusts among the street categories, i.e., the relative abundance in each category (Figure 4B), provided insights into the effects of this physical constraint on locust behavior and flow within the city. Note, for example, that while category 1 streets constitute approximately half of the available space in the New York model (46%), only 20% of the locusts were found to occupy this type of street. Similar trends were observed in the other city models, and this finding was also evident when focusing on only walking locusts (Figure 4C). Note, however, that while Figure 4A shows minor differences among the city models, the results obtained when calculating the time (or frames) spent by walking locusts in the different street categories (Figure 4D) differs among the three city models. For example, in the New York model, locusts spent little time on streets in the narrowest category (Figure 4D, dark color, 2%); however, in the Rome model, locusts spent a much larger proportion of their time in this street category (20%). These findings validate the results shown in Figure 3; in the New York model, locusts showed a clear preference for streets in the widest category (43%), while in the Rome and Cairo models, the locusts spent the most time in the second widest street category (39% and 53%, respectively).

In addition, we conducted an analysis based on the turns or angles in the trajectory direction changes demonstrated by the locusts and their relation to the abundance of city street corners with different turn angles (Figure 5). The city models differ greatly in terms of the

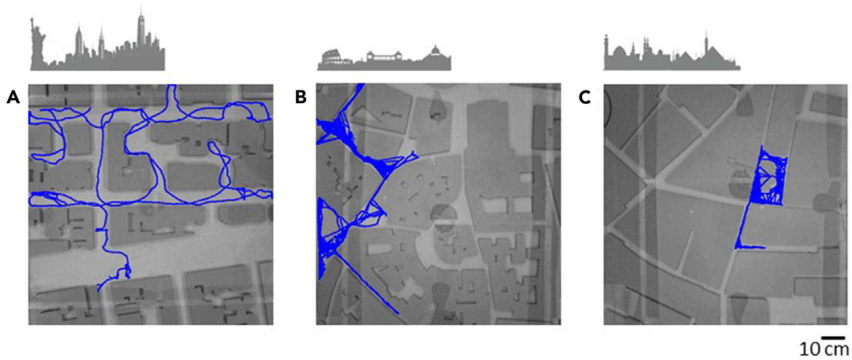

Figure 2. Three examples of the locusts' variable individual locomotion patterns, as demonstrated by the individual insect trajectories

(A) Some locusts explored most of the available space, "roaming the streets" of the model.

(B) Other locusts limited their exploration to a section of the city area, alternating between a few open spaces.

(C) However, other locusts showed a clear preference for a specific favored space within the city model. Although the three examples are from the three different city models, this does not necessarily suggest a correlation between a specific type of behavior and a specific city topology (see text for details).

distribution of corner turn angles (Figure 5A). For example, as expected, the New York City model includes mainly 81–100° corners, while the Cairo model includes many corners with angles of 21–40°. In contrast to this difference, the distributions of actual trajectory changes (turns) made by the locusts moving within each city are surprisingly similar (Figure 5B), implying a far from simple or direct interaction between the city topology and the flow around street corners.

Locusts' collective behavior and city topologies

Finally, we exploited the known tendency of locusts to group and move collectively in clusters of different sizes. We first analyzed the relative abundance of locusts observed in groups (2 or more locusts, walking or standing) on the different street type categories. As shown in Figure 6A, while the tendency to aggregate was somewhat limited by the constraints of the complex city topology, the proportion of clustered individuals among the different street categories differed for each city. Note that in this analysis, walking and standing individuals were both referred to as clustered if they were at a minimal distance from each other (i.e., practically touching for more than 3 s). Intriguingly, the results show that a relatively small proportion of locusts were clustered within the different street categories in the New York model. It should be noted that the street categories were independently defined for each of the city models and that the overall relatively wider streets in the New York City model allowed for higher speeds, fewer obstacles, and increased locomotion and therefore less conjunctions and aggregation. In Figure 6B, we focus on only the walking individuals, utilizing a somewhat different analysis approach: locusts were considered walking in a group if they moved a distance of less than one body length from a neighbor for more than 3 s. In the New York City model, which was characterized by wider streets, most locusts tended to move in clusters (overall, more than 60%), but for the category 4 streets (narrowest), equal proportions of locusts were observed walking in groups or alone. Somewhat unexpectedly, a similar trend, namely, a clear preference to move in groups, was also observed in the Rome and Cairo models, although in these models, most locust clusters were found in category 2 streets. These results also validate the data shown in Figure 4, in which the largest proportion of locusts was observed in category 2 streets in Rome and Cairo.

City typology and flow

We assessed each case as an example of a distinct typology, and our intuitive expectations were to observe a clear relation between the space available to the locusts and the prevalence of collective behavior, e.g., the wider the streets, the fewer twists and turns in the trajectories, and the more coordinated the group motion. Similarly, a city typology with many open spaces should lead to increased aggregation and more synchronized group behavior than a typology characterized by twisting narrow paths. However, our findings were not completely consistent with these simplistic assumptions.

In the case of the Cairo model, which has unique characteristics such as small-angle street corners (Figure 5A), the locusts tended to avoid sharp turns (Figure 5B). While the majority of streets in Cairo are narrow (only 16% are within the widest category), locusts did move throughout the streets, and the second narrowest street category was "popular" for both walking and standing locusts (Figures 4B and 4C). However, the locusts spent most of their time on the wider streets (Figure 4D; 53% of the locusts were in the second widest category), suggesting that open spaces in cities are places of gathering (see also Figure 3).

Rome is characterized by a topology aimed at roaming crowds (tourists and locusts alike). This was reflected by the distributed proportion of locusts among all the city streets (Figures 3 and 4), without a strong preference for any street type (Figure 4). The locusts also demonstrated turn angles that were not necessarily common in the city (e.g., angles of 21–40°). Furthermore, the most conspicuous finding in the Rome model was that many locusts in groups were observed on all street types (Figure 6A).

Finally, in the case of the New York model, which includes wide and orthogonal streets (Figure 4A), the locusts tended to spend more time in the wider streets (Figures 3 and 4D), although both standing and walking locusts occupied all the street categories (Figures 4B and 4C). The

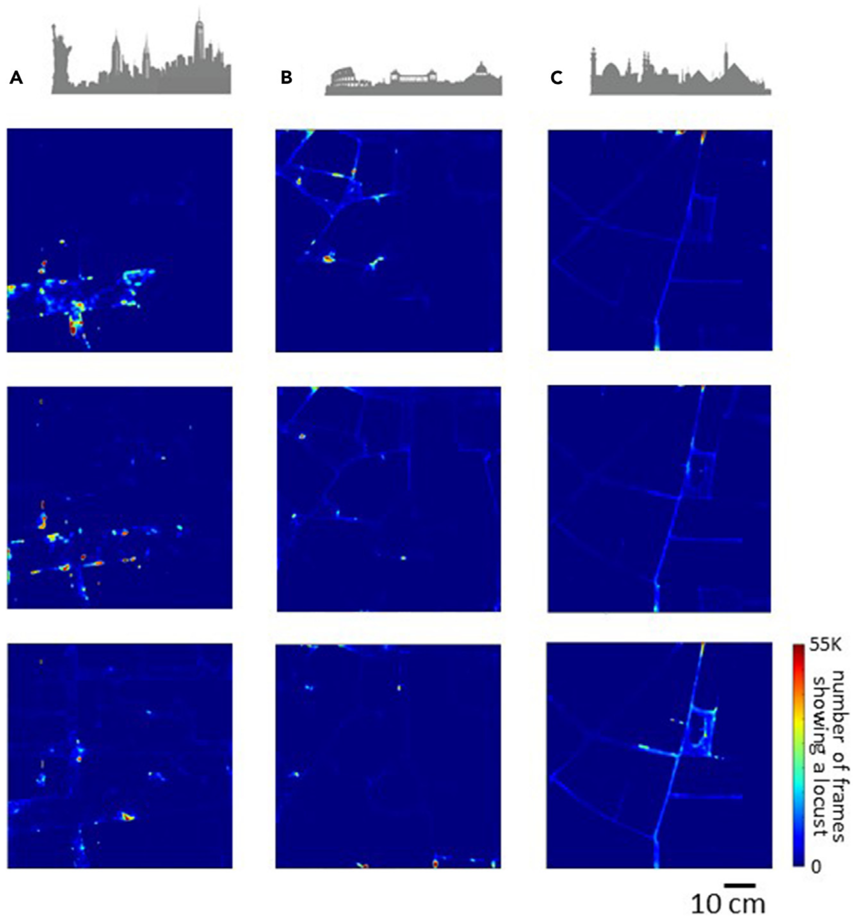

Figure 3. The cumulative occupancy of insects in different parts of the city models

Each column of panels (A–C) represents three heatmaps constructed for three nonoverlapping 30 min segments of an experiment, depicting the cumulative occupancy of insects in different parts of the city models (denoted by number of frames showing a locust). Note the preference of the locusts for specific regions within the city vs. their tendency to explore other regions.

natural inclination of the locusts to strongly favor turn angles in the middle of the angle range (i.e., 81–100°) was well suited to the city's topology, as reflected by the distribution of street corner angles (Figure 5; compare Figures 5A and 5B for the New York results). The previous findings lead to the following observation—while one would imagine that the city topology of New York supports "group walking" and thus collective locust motion, our data suggest that although locusts clearly preferred walking in groups for most street categories (Figure 6B), relative to other city typologies, there were less aggregation in the New York model (Figure 6A).

DISCUSSION

Urban typologies are becoming a focal point in addressing the challenges of both mobility and flow. Typologies are useful in the creation of prototype cities for large-scale future mobility simulations, as cities significantly contribute to global carbon dioxide emissions.[21] We used urban topologies as useful tools for the classification and generalization of innovative spatial solutions and presented a novel approach for studying the interactions between factors related to flow and the structural topology of cities. Although the cases analyzed here were examples rather than a comprehensive urban typologies analysis, the presented data suggest a complex picture. For example, the wide streets of New York should be ideal for collective locust motion, yet aggregations did not form. In Rome, the typical circuits were expected to be hubs of collective motion, but the flow in the city was rather uniform. In contrast to expectations, Cairo was not the least flow-supporting topology. Hence, trivial predictions did not necessarily always hold, and *intricate dynamic interactions were observed between the city and the locusts and between the topology and flow.*

In contrast to previous attempts to address these important questions by employing computer models and simulations, we considered an experimental approach, utilizing physical models of different types of urban environments and live animals engaged in actual physical interactions with city structures. Our methodology had several novel aspects. First, we exploited the natural tendency of the selected animal—locust nymphs—to demonstrate active motion and explore as individuals. We further utilized their strong inclination for aggregation and

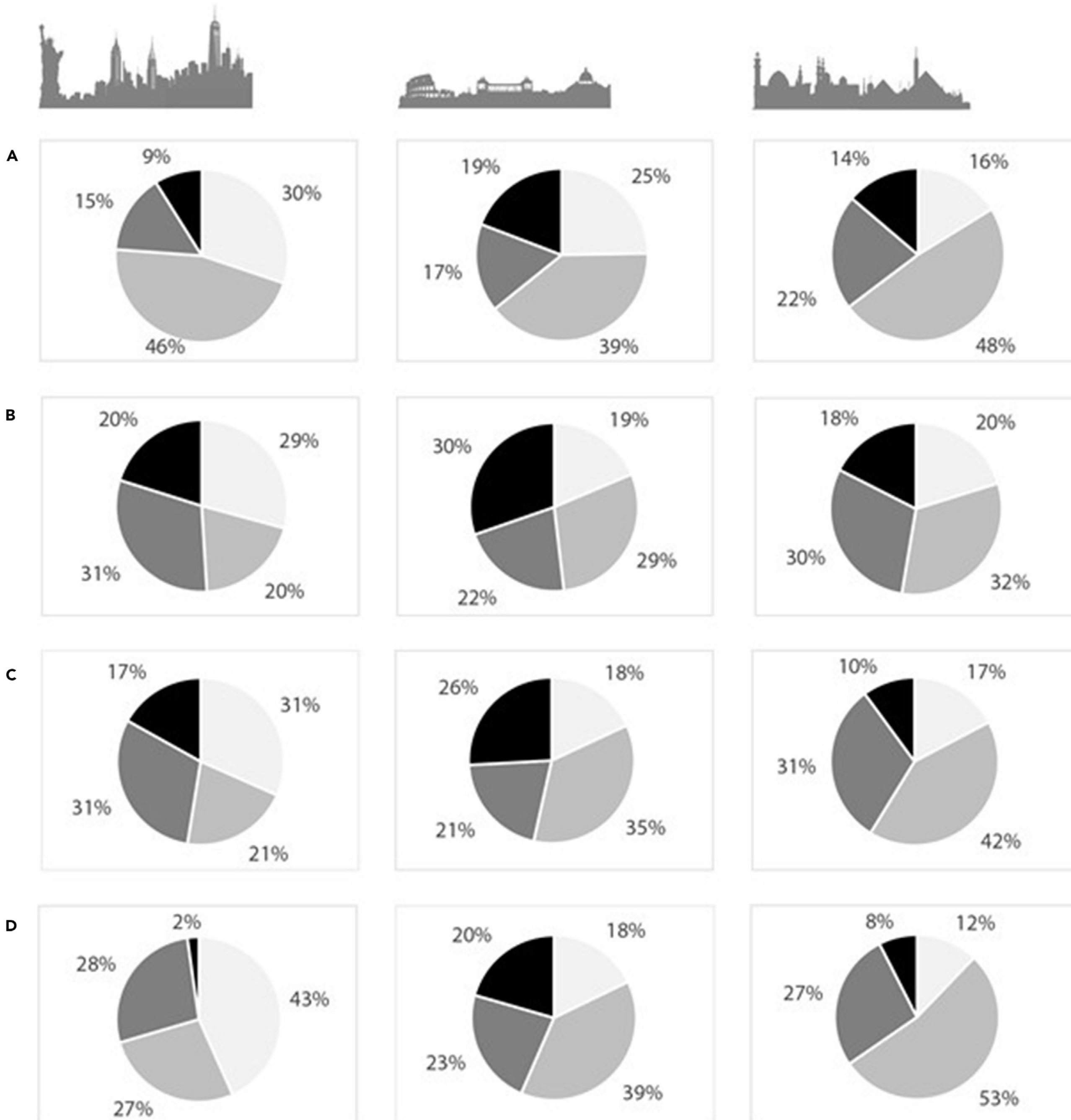

Figure 4. The behavior of the locusts in different street type categories

(A) The distribution of the four street type categories in each of the city models.

(B) The actual distribution of the locusts among the different street categories.

(C) Same as B, but only for walking individuals.

(D) The distribution of time spent walking by locusts in each street type category. Street width color coded from the widest street/space (category 1—light color) to the narrowest street/space (category 4—dark color).

collective motion. The individuals' exploration patterns and the synchronized motion of clusters or groups were strongly dependent on their interactions with each other and with their physical environment, i.e., on the constraints of the specific urban city model. Thus, our approach differs significantly from agent-based computer models (or even from robotic devices moving in the real world). Many unexpected dynamics emerge from the physical interaction between the agents and between them and their environment. These are totally concealed in the

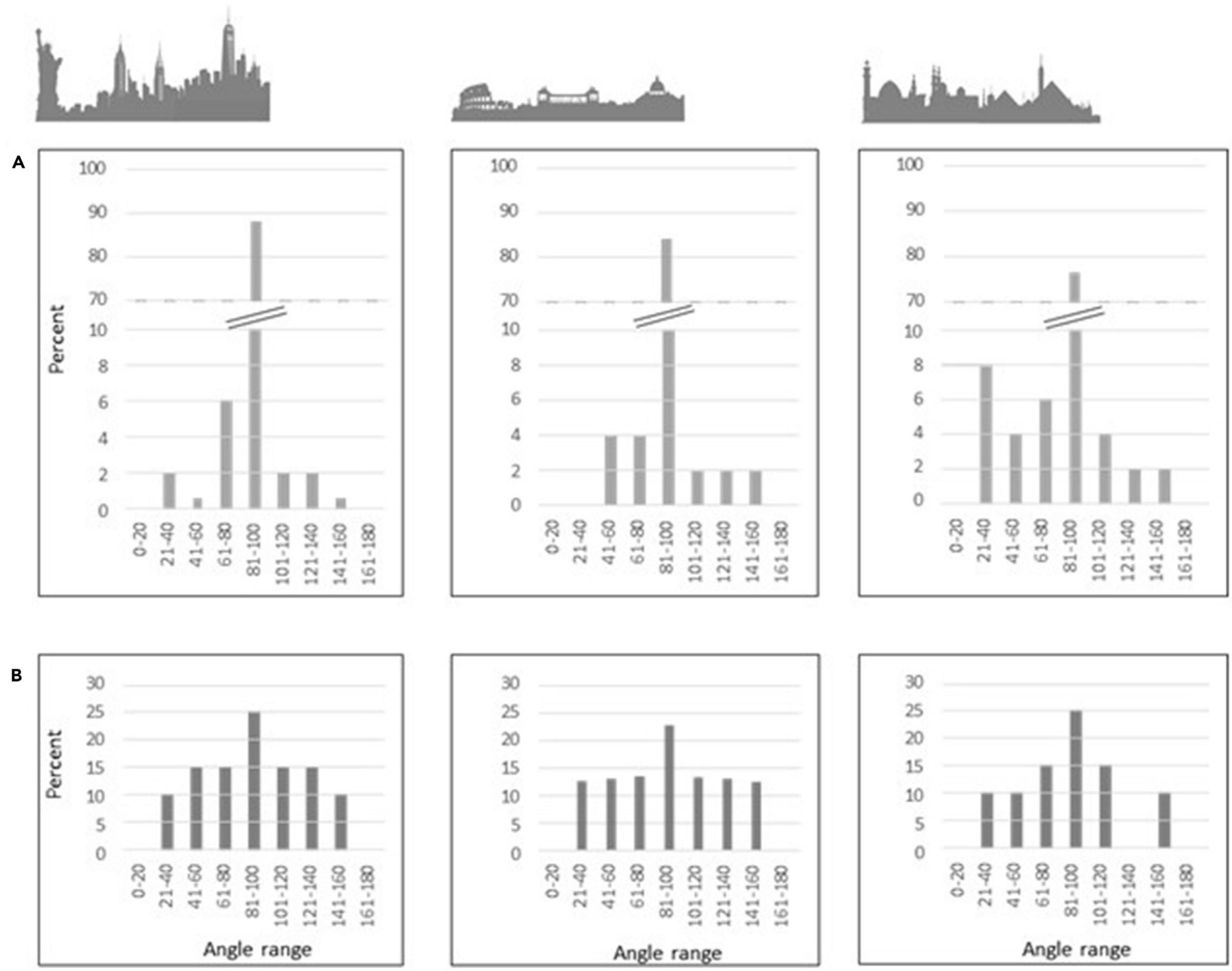

Figure 5. The interaction between the city corner turn angles and the turning behavior of the locusts

(A) The distribution of corner turn angles for the three city topologies.

(B) The distribution of the turn angles performed by the locusts within the city models.

simulation environment. Furthermore, using biological agents adds additional levels of unknown complexity (e.g., the agents' "subjective world") that are impossible to predict and, therefore, to simulate in any virtual model. So, the actual experiments also assist in "learning" the biological agents' behavior (the "biological complexity"), which, in turn, can be implemented in better computer models for future use.

It should be noted that in this work, we utilized locusts merely as a "tool" for investigating urban typologies. Hence, we do not discuss here important aspects of the insects' behavior. Readers are referred to our ample previous studies of locust collective motion, where we focus on the locust behavior per se.[17–20]

Using our methodology, future studies could benefit from varying the number of insects employed in each experiment. The size of the insects can be varied by choosing earlier developmental stages of the locusts (e.g., 3rd or 4th nymphal instars). Furthermore, by using live organisms (rather than simulated agents or robotic devices), we could exploit the rich and intricate aspects and dynamic nature of animal behavior. For example, in the case of locusts, we can use swarming locusts, as reported here, or locusts that were bred in isolation (solitary locusts), which demonstrate stronger repulsion (rather than attraction and collective motion). Similarly, other insects that differ in their capacity to show collective motion can be used. For example, in the case of using ants as the model insect, we could utilize ants that follow each other using pheromone trails or solitary foraging ants. The same principles and approach can also be applied to other, larger organisms (e.g., different species of colonial vs. solitary rodents), with obvious size-related limitations.

Second, dedicated custom measures were developed, which allowed us to obtain quantitative descriptions of the movement- and flow-related behavior. Common parameters used for describing collective animal motion focus on the interactions between individuals and the interactions between individuals and the group. Here, we also focused on interactions with the physical environment. We note, for example,

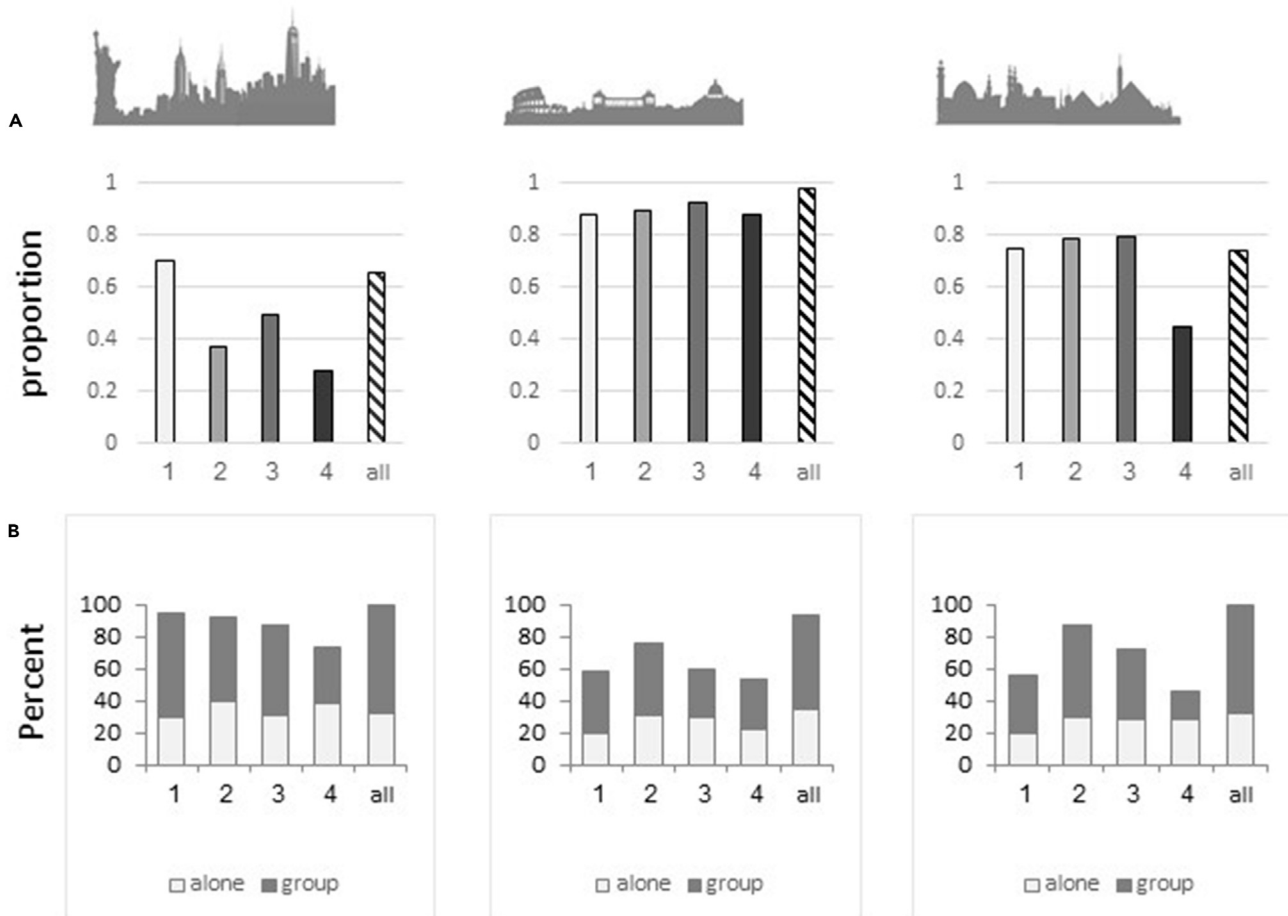

Figure 6. Locusts in groups and clusters

(A) The relative abundance of locusts (walking or standing) observed in groups (>2) for the different street type categories (1–4, from the widest street/space to the narrowest, colors as in Figure 4).

(B) The proportion (%) of walking individuals (out of 100% = walking + standing)—divided into walking alone vs. in a group (>2).

The numbers 1–4 denote the street type. See text and STAR Methods for the analysis details.

the presented data regarding favored vs. less favored regions of the city, showing that locusts preferred to move on streets of specific widths and to gather in open spaces. The analysis allowed us to identify city structures supporting group motion and city structures constraining cluster formation that favored individual walking. Future experiments can explore specific aspects of the urban topology, utilizing carefully constructed models to directly investigate the effect of specific features on the flow characteristics.

Flow is an important factor in the functioning of cities, with typologies playing a significant role in terms of both affecting and managing flows. Our approach can provide two directions for future city development: (1) better understanding of the relations of fast (walking) and slow movements (clustering, standing) in typologies and, thus, planning/adjusting typologies accordingly. (2) Better managing planned and desired aggregation in cities in an age of enhanced urbanization. These directions can complement current work on pedestrian flow on the city's sidewalks and roads.[22–24] Both types of studies focus on the dynamics of self-organized order and how their interaction with the physical environment shapes them. As we show in the current study, these interactions generated some unpredictable dynamics, which is a point worthy of further investigation in pedestrian research.

Finally, in the urban age flow-related questions will continue to occupy policymakers, planners, and scientists. Flows are shaped by the physical layout of cities, affecting human mobility, economy, culture, health, and environment. By impacting CO2 emissions, they significantly influence climate change. Our biodynamic approach considers a missing analytical dimension, allowing us to optimize the relationships between flow and spatial arrays in the development of a sustainable urbanized world.

Limitations of the study

This study utilizes locusts and their strong natural tendency for collective motion as a tool to gain insights into the interactions of urban topology and flow. The urban environments in our study are scaled-down models of distinct areas in real cities. However, it must be noted that no special attention was dedicated to the relative scale of the models and the insects. Hence, the locusts do not serve as proxies for human pedestrians or vehicles traveling city sidewalks and roads (based on their relative size, they are closer to the latter). Accordingly, the locusts are free to roam the streets, limited only by the physical constraints imposed by the urban structures (no traffic laws, etc.). While this approach serves the purpose of our study well, it also underscores the caution required when directly inferring traffic-related conclusions from our findings.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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  - Materials availability
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- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHODS DETAILS
  - Urban simulation
  - Experimental setup and movement recording
  - LocusTracker, general description
  - LocusTracker, technical details, parameters and output
  - Analysis of urban form and flow
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.109922.

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AUTHOR CONTRIBUTIONS

Conceptualization: A.A. and T.H. methodology: A.A., T.H., and R.M.F. investigation: M.G. formal analysis: M.G. and R.M.F. visualization: M.G. and R.M.F. writing—original draft: A.A. and T.H. writing—review & editing: M.G., R.M.F., A.A., and T.H.

DECLARATION OF INTERESTS

All authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental models: Organisms/strains		
Desert locusts	Our breeding colony	
Other		
See https://github.com/RoeeFrancos1990/LocusTracker For our custom developed tracking and analysis code		

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact Prof. Amir Ayali (ayali@post.tau.ac.il).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data reported in this study is available from the lead contact upon request.
- All original code developed in this study is available by the lead contact upon request.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Desert locusts, *Schistocerca gregaria* (Forsskål), reared in our breeding colony at Tel Aviv University School of Zoology, were used in the experiments. The insects were maintained at a high density, with more than 100 animals in 60-L cages, under a 12 h:12 h light/dark cycle, at a temperature of 30°C and 30–65% humidity. The locusts were fed wheat seedlings and dry oats daily. All experimental locusts were last instar larvae, the offspring of many generations of gregarious locusts reared in these conditions.

METHODS DETAILS

Urban simulation

Scaled-down (1:200) physical models of carefully selected city regions were constructed for the study. The models capture the characteristic spatial morphology of the city. Each model measures 120 × 120 cm and replicates 200 m^2 in the city. The buildings and other structures were 3 cm high to allow the insects to move freely. The streets were lined with a homogeneous white background, while the buildings and other structures were painted dark gray. The models were wholly encased in transparent plexiglass. The percentage of areas of the model free for hoppers to walk in was as follows: New York- 53.08%; Rome - 30.36%; Cairo- 21.52%. Further quantitative features of the city models that need be calculated include the total active area (=streets), the street types, which are categorized by their relative width (1 = widest, 4 = narrowest), and number and location of corners.

Experimental setup and movement recording

The experimental arena (i.e., city model, as described above) was located in a dedicated behavior room. LED light sources were placed in the arena to ensure that the floor was evenly lit. A group of 50 fifth-instar desert locusts were introduced into the model via a small opening in one of its walls (randomly selected) and allowed 15 min to acclimate. A video camera (Sony FDR-AXP35: 4K Ultra HD) was positioned above the arena to continuously capture the locusts' behavior throughout an uninterrupted, 4-h experiment (in 30 FPS). The video files were then transferred to a PC computer for offline analysis using LocusTracker, a custom-designed multitarget tracking framework, which generates a dataset including all locust locations in every frame, thereby allowing researchers to track the locust movement trajectories (see details below and in the supplementary text).

LocusTracker, general description

All movements of each individual locust were monitored and tracked, as described above, and the data were used to analyze and predict the locust trajectories using an algorithmic pipeline based on the principles of tracking by detection and association for long time horizons without placing physical markers on the individual locusts. "Tracking by detection" means that the potential locations of the locusts are identified in each time frame. The detected locations are then matched to the previous locations where the locusts were detected, enabling researchers to generate continuous locust trajectories throughout the experiments.

The LocusTracker consists of six main modules (see further details below).

1. The background subtraction module is used to detect the locations of the locusts in the model city based on the difference between the current frame and a reference image of an empty city that does not contain locusts. This method reduces the sensitivity to illumination changes that occur in different environments and different lighting conditions.
2. The blob locust detection module detects and identifies locusts or clusters of locusts. The input to this module is the foreground image generated by the background subtraction module. Locusts are detected based on various properties, such as shape and size.
3. The locust trajectory association module receives input in the form of candidate points that represent the center of mass of each detected locust in the current frame, as well as information regarding the detected locations of the locusts in previous frames. The purpose of this module is to determine how the newly detected potential locations of the locusts are associated with the previous trajectories of other locusts. Matching between candidate points and trajectories is based on a set of logical constraints inferred from observations of the movement patterns of locusts.
4. The locust cluster analysis module aims to identify whether detected locusts are part of a locust cluster, and if so, how many locusts are part of the detected cluster. This module is also responsible for managing the IDs of locusts that form, enter and exit existing clusters to continue tracking the locusts as individuals when they leave the cluster. When locusts are part of a cluster, all locusts in the cluster are assumed to be located at the same point (at the center of the cluster).
5. The extraction module isolates meaningful parameters for statistical analysis and evaluation. The parameters include but are not limited to the locations of the locusts, whether the locusts are stationary or moving, movement speed, movement angle, whether the locusts are part of a cluster, and the proximity to a detected corner.
6. The visualization module depicts the extracted results in several ways to better understand the locusts' movements and behaviors in the environment. The outputs of this module include a heatmap showing the magnitude of the locust concentrations in different parts of the environment as a function of time, visualizations of the trajectories of individual locusts during the experiment, and a video file showing the movements of the locusts over time.

LocusTracker, technical details, parameters and output

The output of the LocusTracker software is provided in the form of tabular data, containing the computed parameters used for statistical analysis, as well as several visual outputs that assist in evaluating the obtained results. The information provided below includes the extracted parameters that are used in the statistical analysis and the methods used to calculate them.

Output files format

The corresponding movement files for each locust are saved in a folder containing an excel file that is associated with the movement of each individual locust. Each of the generated files contains information such as.

- Frame number in which the locust was detected.
- Locust ID number.
- Coordinates of center of the blob representing the locust in that frame.
- Angle at which the locust is headed based on a coordinate system centered at the center of locust's blob.
- A flag indicating whether the locust is considered to be moving in the current frame.
- The locust's speed in cm/sec.
- A Boolean flag indicating whether the locust is a part of a locust cluster in the current frame.
- The number of locusts corresponding to the observed locust in the current frame. If this number is 1 - the locust is not a part of a locust cluster and in case it is more than 1 - the number of locusts in the calculated area is based on the ratio between the area of the cluster and the typical area of a locust.
- A Boolean flag indicating if the locust is near a corner in the current frame.
- The area type in which the locust is currently located.
- The distance a locust advanced up to the current frame.
- The time intervals at which locust are stationary.
- The time intervals at which locusts are moving.
- The IDs of other locusts that the locust is marching within the current frame.

Additionally, a combined excel file that integrates the information of all locusts is generated for easing the analysis that follows.

Visual outputs

The extracted results are visualized in several ways in order to better understand the movements and behaviors of the locusts in the environment. These outputs include.

- Heatmap showing the magnitude of the concentration of locusts in different parts of the environment as a function of time.
- Visualizations of the trajectories of individual locusts during the experiment.
- Video file showing the movements of locusts across time.
- Technical Details

We use several preselected parameters in order to perform the trajectory analysis from the recorded videos. The parameters and the values are provided below.

- Maximal movement in a single frame- the maximal movement possible for a given locust- this value was chosen as m0.2 *c*.
- Minimal Euclidean distance between detected locusts - this distance corresponds to the locust size and is used to identify individual locusts.
- Maximal number of tracked locusts- In order to allow the generated locust trajectories to extend the duration of the recorded video, we use prior knowledge on the number of locusts in the environment. In all considered experiments this number was selected to be 05.
- Movement threshold in (cm/sec)- If exceeded then the locust is considered to be moving, this parameter is used for classification purposes. The chosen value in the conducted experiments is c0.25 *cm*/*se*.
- Locust blob size- based on the distance of the camera and the arena the average locust blob has a radius of 3.5 *cm*. If animals having different sizes are being observed, or the arena is photographed at other distances then the average size of the observed animal needs to be assessed and provided to the model in order for it to accurately assess locations of observed individuals and density of entities inside each detected cluster.
- Heading angle- In order to provide the association module a parameter that filters motions of locusts based on their heading angle, a maximal turning angle of 3° is used to connect current and past locations of detected locusts.
- Corner distance threshold- A distance threshold measured from the center of the blob representing the locust is used to determine if a locust is near a corner. This information is later used in the analysis to determine if the movement choices a locust makes depend on its proximity to corners. The chosen value in the experiments is a distance less than 1 *cm* to be considered near a corner.
- Marching together thresholds- The time threshold for locusts to be considered as marching together was selected as if they are in the proximity of one another for more than 3 *sec*. Locusts are considered to be in the proximity of one another if their distance is less than 5 *cm* apart.

Extraction of parameters for statistical analysis

Corner detection module-corner detection is a useful technique in computer vision that is used to extract points of interest in an image. According to our scheme, we wish to detect and identify corners in the experimental arena (city model) in order to determine if the presence of a locust near a corner influences its movement decision making mechanism. The basic concept in corner detection is to classify a point as a corner if two dominant edge directions exist in a local neighborhood of the point. A point is classified as a corner when both eigen values of its second moment matrix are larger than a chosen threshold. Based on this selected threshold, we are able to extract the locations of corners in each of the city models using the Harris corner detector. This information is extracted from images of the city models prior to the introduction of the locusts.

Analysis of urban form and flow

Following the tracking process, we analyze five randomly chosen, nonoverlapping 30-minute segments selected from two four-hour movies for different experiments in each city model. The following parameters are calculated for the entire arena as well as for each street type:

- Fraction of walking – the number of frames/seconds an animal walked divided by the total number of analyzed frames.
- Walking bout duration – the time an animal walked continuously between one pause and the next, averaged for all walking bouts.
- Walking bout frequency – number of walking bouts, averaged for all individuals.
- Walking distance – total and per bout (in cm), averaged for all individuals.
- Walking speed – averaged for all experimental animals and analyzed frames.
- Pause duration – the time an animal did not walk between one walking bout and the next, averaged for all pauses.
- Number of turns and absolute turning angle, averaged for all individuals.
- Clusters (defined as more than two locusts in contact), average number and size.

QUANTIFICATION AND STATISTICAL ANALYSIS

Statistical significance of the difference between any two data groups was demonstrated using Chi-square-test. ANOVA was used for multiple comparisons. For all the experimental results shown, the error bars indicate the standard deviation and the details of the statistical tests are presented in the figure legends.