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Research Paper

Pigs in space: An agent-based model of wild boar (*Sus scrofa*) movement into cities

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ABSTRACT

Last decades saw a dramatic increase in wildlife populations within urban areas. Policymakers seek to minimize human-wildlife conflicts resulting from overabundance of species, such as wild boars (*Sus scrofa*). To this end, there is a need to understand the drivers governing infiltration of wildlife into cities. In this paper we study the availability and distribution of food resources in urban areas as driver of wild boar movement patterns. Based on the optimal foraging theory, we utilize an agent-based simulation model to investigate the ever-growing infiltration of wild boars into some cities. We apply the model to an artificial city that mimics the landscape of the city of Haifa. Manipulating food availability and relative resistance costs of different land-covers we demonstrate that infiltration of boars depends on population size of wild boars and on the amount and spatial distribution of attractors (e.g., food). Model outputs for likely sets of parameters demonstrate good correspondence to the reports of boar observations within the city of Haifa, Israel, where the porosity of the urban fabric and the connectivity of open space patches provide a trail network that makes food throughout the city accessible at a relatively low search-cost. Our results indicate that land cover and food patterns determine critically boars' foraging movement and infiltration into the city. The proposed modeling framework provides a tool to investigate wildlife management policies that aim at reducing people-wildlife conflicts in cities.

1. Introduction

Urban expansion seems to encroach nature continuously when buildings, areas in-between buildings, and roads are grouped together. However, at a finer resolution the urban fabric is porous and contains gaps of unbuilt green open spaces (Czamanski et al., 2008; Toger, Malkinson, Benenson, & Czamanski, 2015) of small and large vegetated gaps between buildings and city parks. These urban open spaces (Urban Green Spaces – UGS, as in Aronson et al., 2017) often contain both native and nonnative flora and fauna (Aronson et al., 2014; Matthies et al., 2013; VanDruff & Rowse, 1986). Urban green spaces provide habitat to a number of wildlife species, including foxes (*Vulpes vulpes*; Devenish-Nelson, Harris, Soulsbury, Richards, & Stephens, 2013), bears (*Ursus arctos*; Sato, 2017), bobcats (*Lynx rufus californicus*; Cypher et al., 2010), coyotes (*Canis latrans*; Cypher et al., 2010; Weckel, Mack, Nagy, Christie, & Wincorn, 2010) and wild boars (*Sus scrofa*; Licoppe et al., 2013; Stillfried et al., 2017).

Wild boar (*Sus scrofa*) is one species of particular concern in urban areas. Across Europe, North America, parts of Asia, Australia and elsewhere, wild boar populations have increased dramatically during the last few decades (Licoppe et al., 2013). In fact, *Sus scrofa* is an overabundant species in more than 60 urban areas around the world (Licoppe et al., 2013). Specifically, this species is involved in vehicle traffic accidents (Thurfjell et al., 2015), spreads diseases (Gortázar, Ferroglio, Höfle, Frölich, & Vicente, 2007), and has negative effects on plant and animal species richness and abundance (Genov & Massei, 2004). Because of these problems, a variety of management approaches are being considered to regulate wild boar populations, ranging from attempts to completely eradicate them locally to reduction of population size once population or damage thresholds are exceeded (Licoppe et al., 2013; Barshaw, 2012). However, to date, none of the control methods have been deemed successful.

The increasing presence of wild boars in urban areas is associated with behavioral changes. They are increasingly nocturnal and move further into cities due to the patchy nature of the habitat (Podgórski et al., 2013). In general, patch size, habitat heterogeneity, and

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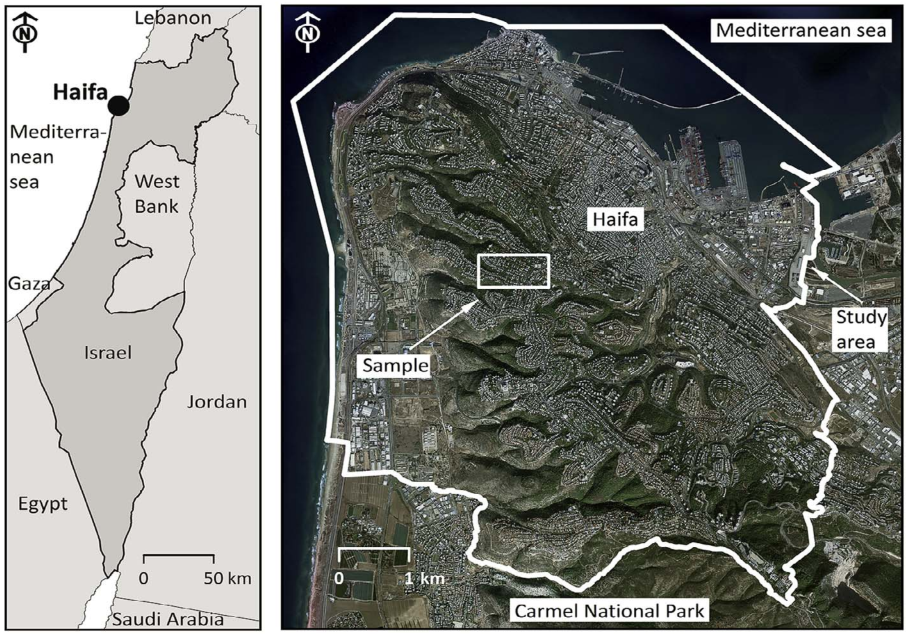


Fig. 1. The Haifa region with the simulation area (white polygon). This part of the city is characterized by the mix of naturally vegetated gullies, constructed ridgelines and residential construction.

connectivity decrease towards the city center while patch density increases (Goddard, Dougill, & Benton, 2010). Furthermore, roads result in habitat fragmentation and isolation as well as increased mortality from vehicles, particularly in the case of large mammals, (Rudnick et al., 2012). Some urban morphologies, such as Haifa, have networks of corridors and open patches that make the city quite porous for large mammals (Toger et al., 2015). These networks provide relatively easy access to the food sources required by wild boars. Boars' diet is a major determinant of their foraging movement (Holm, Jensen, Pedersen, & Ladewig, 2008) and exhibits seasonal changes with variation in food availability (Massei, Genov, & Staines, 1996). Urban residential and commercial neighborhoods provide food resources that supplement food resources found in natural and semi-natural areas within and around cities. The presence of garbage, in particular, can provide a calorie rich and readily available resource. The distribution of food resources in space determines the exploitation-exploration trade-offs between costs in energy expenditure and risk of predation versus potential benefits of finding resources or mating partners in the target location (Fahrig, 2007). While some species make non-optimal movement decisions (Fahrig, 2007), wild boars are remarkably adaptive and opportunistic omnivores with high cognitive abilities.

Given the rapid and significant increase of wild boar presence in urban ecosystems it is important to understand better the possible drivers governing boar movements in them. Specifically, we sought to answer the following questions: How do land use and land cover properties affect the distance and frequency of wild boar movements in cities? Are we able to represent, quantitatively and adequately, the phenomena of wild boars' infiltration into the city Haifa? Given a particular landscape structure, how does availability of food sources affect the infiltration of wild boar there? We follow Luniak (2004) and Charnov (1976), and hypothesize that animal movement is in response to trade-off between energy acquisition versus perceived mortality or predation risk and energy expenditure. Accordingly, we develop an agent-based simulation model of their foraging movement based on the optimal foraging theory combined with a landscape connectivity approach. We employ the model to understand the management strategies that would minimize boar-human conflicts.

2. Methods

2.1. Study area

To address our main research questions, we evaluated wild boars in Haifa, Israel. Haifa is the third largest city in Israel with a population of ~270,000 and metropolitan area of more than a million people (CBS, 2009). The city covers 65.2 km^2 (Haifa Haifa Municipality, 2008) on Mount Carmel, on the Eastern coast of the Mediterranean Sea (Fig. 1), extending from sea level to an elevation of approximately 450 m.

Haifa is a complex mosaic of various building types, intertwined with vegetated gullies, or ravines (wadis), bounded by the Carmel National Park to the south. The semi-natural open space in Haifa consists mostly of rocky slopes, covered with Mediterranean scrubland and woodlands of oak, pine, and *Pistacia* species communities, remnants of semi-natural forests, as well as planted pine stands. Various wild mammal species are found within the city boundaries, including badger (*Meles meles*), fox, wild boar, jackal (*Canis aureus*), mongoose (*Herpestes ichneumon*), rock hyrax (*Procavia capensis*), and porcupine (*Hystrix indica*) (Broitman et al., 2017).

Our research builds upon previous studies of open green spaces in Haifa (Toger et al., 2015; Czamanski, Malkinson, & Toger, 2014) showing that despite the decreasing total amount of open spaces and their increasing fragmentation, many open-space patches remain and their network is sufficiently connected to facilitate movement and habituation by wild boars. In recent years, the presence of wild boars has become an increasingly troublesome issue for Haifa residents. During their nightly search for food, wild boars infiltrate from the city's outskirts into the city's built areas, including the inner neighborhoods. Some Haifa residents view this infiltration as an opportunity to interact with wildlife, while others see this it as a nuisance (Barshaw, 2012).

2.2. An agent-based model of wild boar foraging in Haifa

We assume that the abundance of food resources acts as an attraction force to pig movement, whereas human presence and activities act as a repulsive force for their movement. Hence, the presence of humans increases the cost of animal movement through urban space. By incorporating these juxtaposed forces, we identify the parameter values

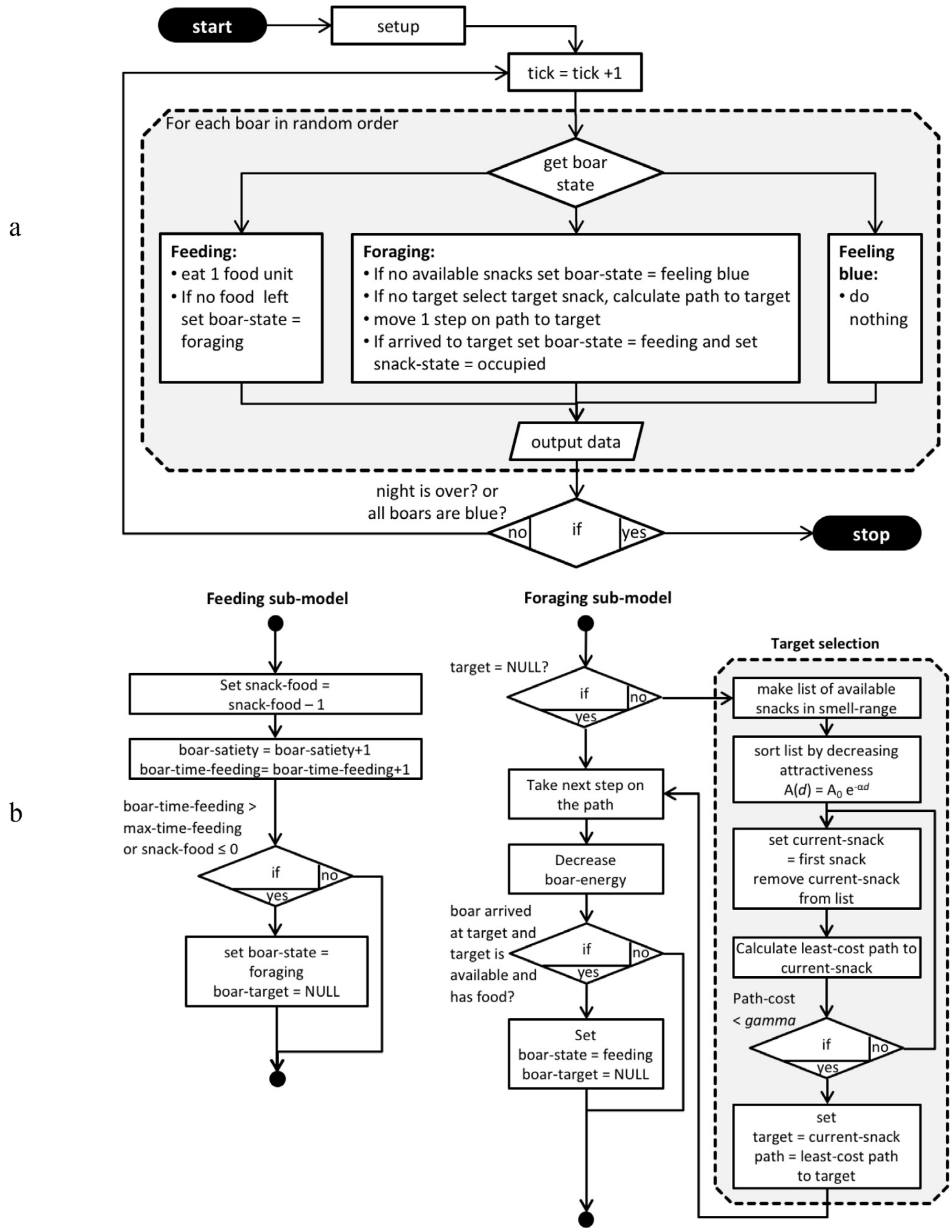


Fig. 2. The flow charts of the (a) main model, and (b) feeding and foraging sub-models.

that make the city an attractive alternative to foraging in natural areas and investigate the depth of boars' infiltration into the city. Our model simulates foraging movements of wild boars across the urban areas. For modeling purposes, we ignore food resources within open spaces that are rich in shrubby vegetation and provide ample shelter to the animals. Observations show significant presence of wild boars in Haifa urban areas (Section 2.8). We thus assume that boars spend their day in open spaces outside the urban area, and perform foraging sallies into the city during the night.

Wild boars spend 40–70% of their daily activity budget on foraging (Blasetti, Boitani, Riviello, & Visalberghi, 1988). Typically, wild boars' movement speed is 2–5 km/h, while they are capable of travelling over open ground at a speed of up to 40 km/h. Large individuals can jump over barriers of up to 1.5 m, or traverse water bodies up to 9 km across (Baskin & Danell, 2003). Wild boars are gregarious animals with social hierarchy governing their spatial behavior. Specifically, they form sounders of 5–30 individuals, dependent on reproductive activities (Oliver & Leus, 2008) and communicate using scent, sounds and visual cues. In our model, we exploit the fact that boars possess high olfactory and cognitive abilities and detect food resources at a considerable distance (Kornum and Knudsen, 2011). We also assume that boars' perception and environment do not change because of increased tameness and postpone the explicit study of boars' ability to memorize and repeat the paths between food sources. Formally, we assume that the boars are able to take a close to optimal path between the food sources. In reality, these paths cannot be established without multiple trials and errors and the boars should be able to repeat them in consecutive days based on memory, scent marks or both. The model focuses on boars' choice of attractive food sources and movement between these sources. The simulation is implemented in the NetLogo modeling environment (Wilensky, 1999).

Table 1
LULC classes for Haifa and the corresponding cost/m of crossing the 5 × 5 cell.

LULC	Description	Cost/m	Category
Forest	Semi-natural and planted forests and woodlands	0.001	Open Space
Shrubs	Mediterranean scrubland		
Grassland	Herbaceous vegetated areas		
Orchard	Vineyards and orchards	0.1	Transit
Garden	Managed vegetated areas: parks, gardens, lawns, etc.	0.25	
Wasteland	Garbage, dunes, beach, mines, wasteland		
Fallow	Abandoned and fallow fields		
Backyard	Backyards, squares, logistic spaces around buildings	0.5	
Field	Cultivated fields		
Dirt road	Unpaved roads		
Foot path	Paved footpaths		
Trail	Unpaved footpaths		
Transport	Railroads, parking	0.75	
Roads	Paved roads		
Buildings	Buildings	∞	Obstacles
Industry	Industrial areas, exurban commercial areas		
Construction	Construction sites		
Agricultural built-up	Greenhouses, warehouses		
Water	Water		

2.3. Model overview

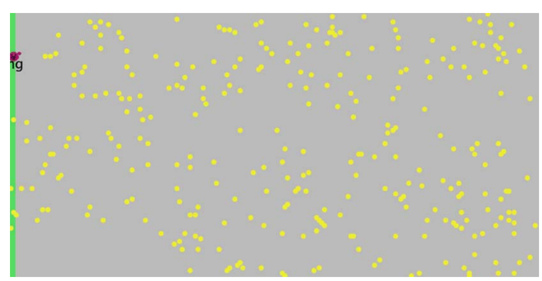
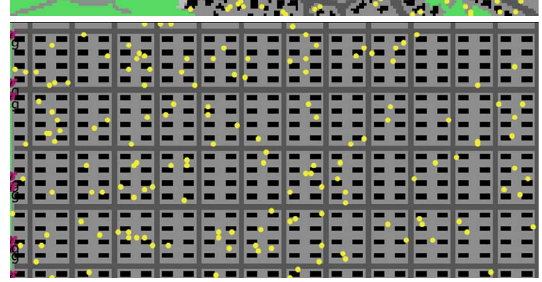
Our agent-based model simulates *boars* that are located near the boundary of the city's built area at dusk, infiltrate the built-up areas to obtain/consume food sources (henceforth *snacks*), move between the *snacks*, and leave urban area at dawn to hide and rest outside during the day. Each boar-agent can be treated as a sounder of females with offspring or as a solitary male. The simulation night lasts 10 h and proceeds by *ticks* (τ) of 1 min (600 ticks per night).

We assume, in accordance with the Optimal Foraging Theory (Charnov, 1976), that boars are goal-oriented, aiming to optimize their food intake at a minimal cost. At each *tick,* every *boar* takes one or more actions depending on its *state*: *feeding, foraging*, or feeling *blue* (Fig. 2), where: *Feeding* (the boar is at the snack): and the amount of food is decreased by 1 unit/tick; *Foraging*: a target snack is chosen and the individual moves 1 step towards it; *Blue*: no available snacks are detected, the individual boar is ignored until the end of the night.

2.4. Boars-Food interaction

Boar food sources are plentiful in Haifa, such as garbage bins, cat-feeding points, litter, etc., (Barshaw, 2012). During the dry season leaks in backyard irrigation and AC drainage provide water for boars. In our model, the *boars* detect *snacks* from a distance by smell. The intensity of the snack's scent depends on the amount of food at the site and diminishes with distance. Snack *attractiveness* (A) is given by exponential distance decay function $A(d) = A_0 \exp(-\alpha d)$, where d is the aerial

Table 2
The characteristics and spatial representation of the simulation scenarios: (a) Garden, (b) Haifa and (c) Synthetic.

	Name	LULC	γ_{max}	Landscape configuration (yellow points represent randomly located snacks)
1	Garden	Homogeneous, easy for traversing landscape	0.3	
2	Haifa	Represents part of the Haifa urban area that is marked by the white rectangle in Fig. 1, a typical neighborhood in the city	Haifa1 $\gamma_{max} = 0.3$ Haifa2 $\gamma_{max} = 0.6$	
3	Synthetic	A synthetic representation of a typical neighborhood lacking open spaces, repeats Haifa's Naveh Shaanan neighborhood: buildings (18%), roads (21%), backyards plus garden (61%). Distance between buildings and a number of buildings in a block (8) is typical for this neighborhood	various γ_{max}	

Cost legend

0.001 Open space · 0.25 Garden · 0.5 Backyards · 0.75 Roads · ∞ Buildings

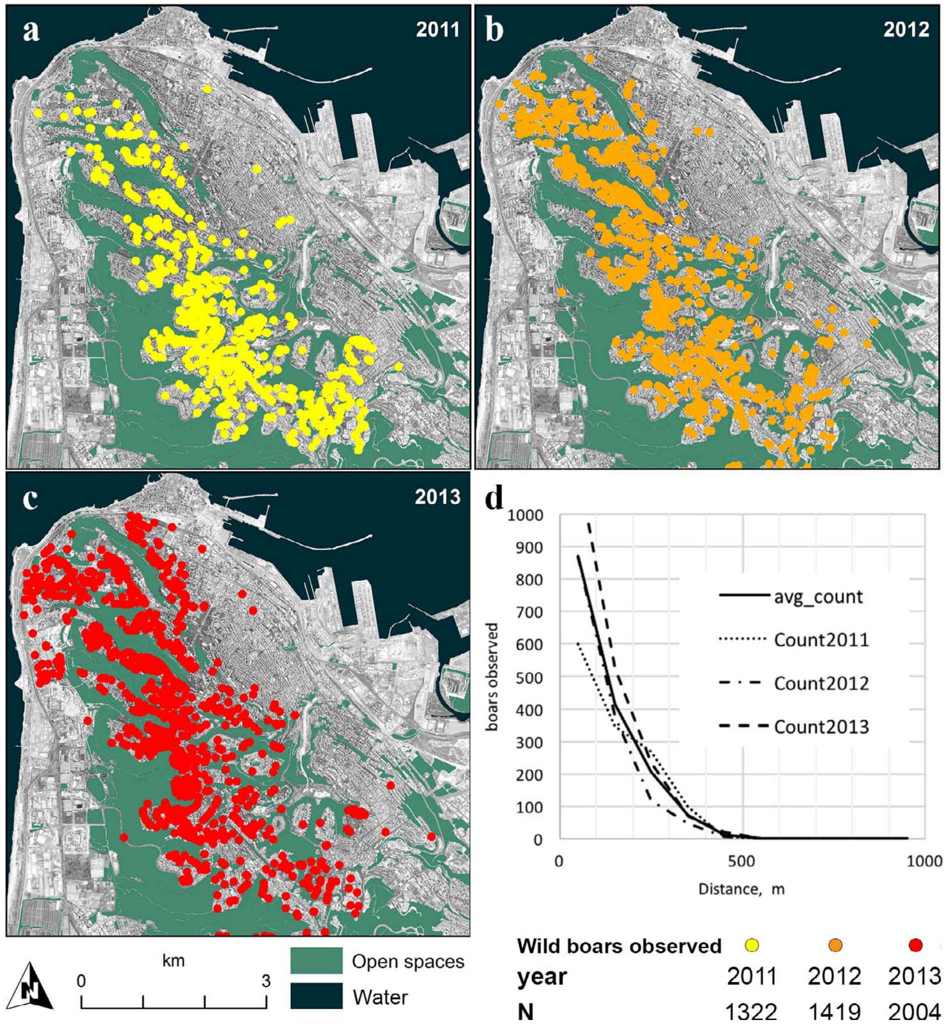


Fig. 3. Wild boar sightings recorded by Haifa municipality, (a-c) maps for the years 2011–2013 and (d) the number of observations as dependent on infiltration distance by years and average over years 2011–2013.

distance (m) from the boar's current location to the snack, A_0 is the amount of food at the snack, and α is the rate of scent decay. In what follows, α is set to decrease attractiveness 10 times for every 25 m. Attractiveness is set to zero when d is above a threshold d_{max} (here 250 m).

The foraging boar selects the snack (i) of maximal attractiveness and estimates the least-cost-path to this snack (we apply the A^* algorithm), assuming that the neighbors of a given patch are 8 cells of the Moore 3 × 3 neighborhood. If the per-cell cost of this path is below γ-threshold (described below) the boar starts moving to the snack, otherwise the next best snack is selected until the snack with the per-cell travel cost below γ is found.

By means of scent and sound, boars are aware whether other individuals occupy the site. They do not share food sources. If a boar agent occupies a site, other boars are unable to join the feeding and have to search for other snacks. Boars feed, consuming 1 food unit per tick, until the snack is depleted, following that decreased predator vigilance was observed in feeding urban animals in general (Sol, Lapiedra, & González-Lagos, 2013) and because wild boar's natural predators are absent in Haifa in particular.

2.5. Boars-Landscape interaction

The urban landscape is rich in food and water resources as well as risks and disturbances for wildlife. A foraging animal in a patchy landscape optimizes energy gain from food intake versus the cost (or risk) of movement (Charnov, 1976). Moreover, the movement paths are less sinuous in a high-risk environment (Fahrig, 2007). In our model we assume that the urban landscape is a high-risk environment known to the boars from previous foraging and thus the *boars*' movement follows shortest (least-cost) paths. The least-cost path is determined over a resistance (*cost*) surface derived from land-use/land-cover (*LULC*) data (see below). The landscape comprises 5 × 5 m square cells (*patches*) each with a *cost* attribute that represents perceived risk of movement across the cell due to potential risks (e.g., crossing roads).

For wild boars, the disturbance avoidance is linked to their habituation to humans (Licoppe et al., 2013). In order to simulate boars' avoidance of dangerous environments we characterize the boars' possible paths by parameter γ – the average cost per meter of a path length, and establish the maximal value of γ, γ_{max}, for which the path is useable for a boar. Higher values of γ_{max} enable higher variety of path choices and thus less restricted movement through the landscape. The range of γ values is defined by the heterogeneous Haifa LULC that includes semi-natural wadis, urban gardens, parks, backyards, buildings and roads.

Haifa's urban land cover pattern was depicted based on a 2012 aerial photograph that was manually vectorized (Israeli Transverse Mercator projection - ITM, EPSG:2039, LULC vectorized based on aerial photo with 0.25 m cell, and rasterized to 5 m cells), classified into 19 LULC types, and then rasterized using the majority rule into 5 × 5 m cells (Table 1). This pattern served for establishing *cost of crossing* the

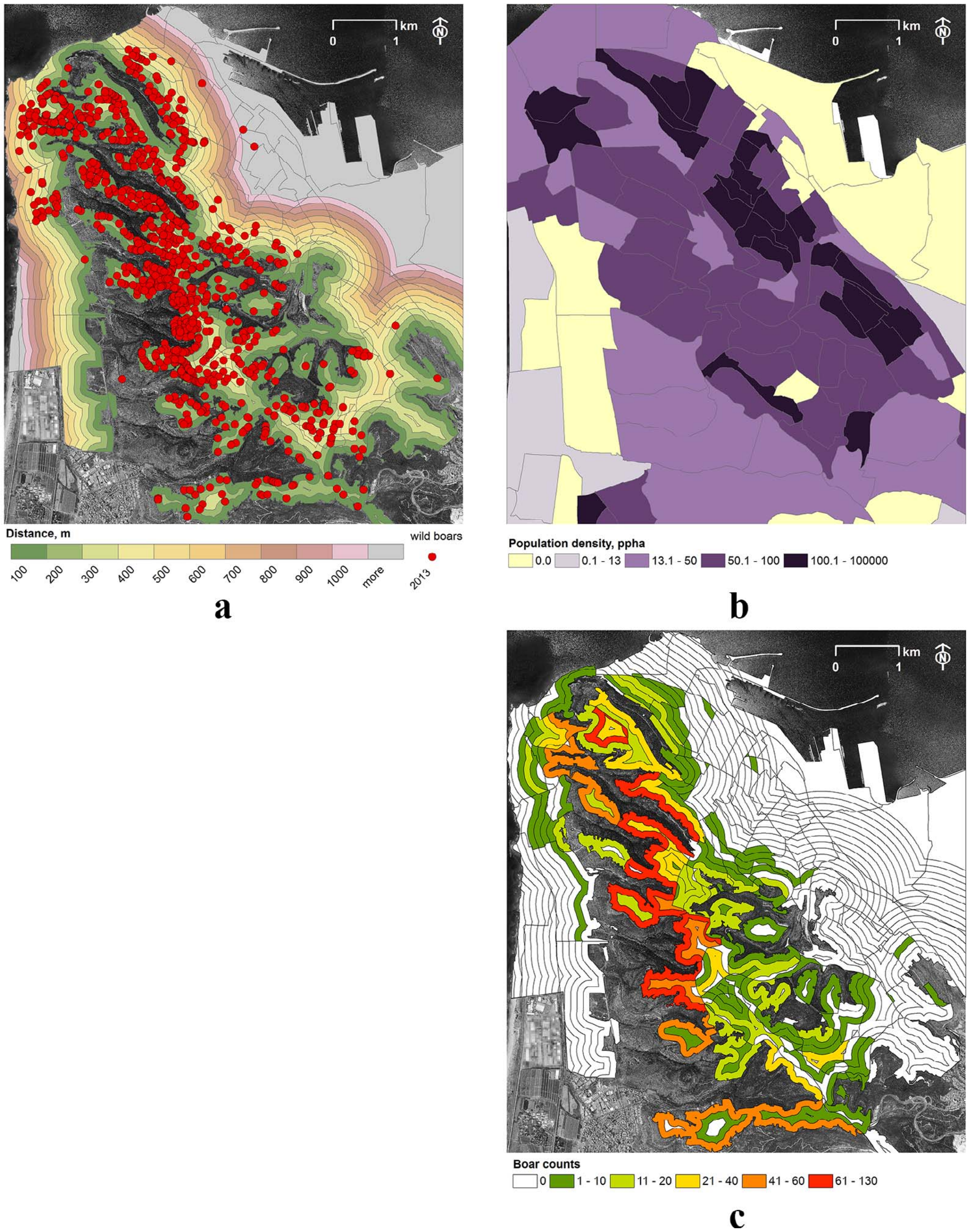


Fig. 4. Haifa boar sightings: (a) Points of where the boars were observed and 100 m equidistant lines from the urban fringe into the Haifa built-up area; (b) Per ha population density by Haifa statistical areas (CBS, 2009); (c) Number of boar sightings per 1000 residents.

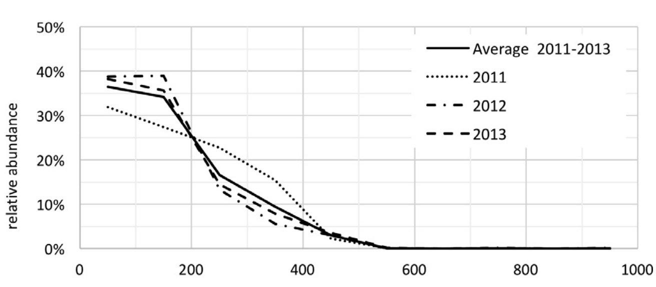


Fig. 5. Relative abundance of boars, by years and averaged as dependent on the distance from the closest outer open space.

cell. Following (Rudnick et al., 2012), we consider cost as a combined measure of disturbance from human activities (perceived risk of movement) and energy expenditure of a boar (Spear, Balkenhol, Fortin, McRae, & Scribner, 2010) and establish the cost based on the LULC classification (Zeller, McGarigal, & Whiteley, 2012). Specifically, we set the cost of resistance based on the Naali's (2009) index of traverse ability for the porcupine: 0.001/m for natural areas and olive groves, 0.1/m for orchards and 0.25/m for fallow crops areas. We exploit porcupine's costs as conservative estimates of cost for boars, which are less averse to human activities. We further assume that for a boar the cost of crossing a backyard is 0.5/m, twice as hazardous as crossing a fallow agricultural field, while crossing a road is 50% more hazardous than a backyard, 0.75/m. The resulting values are presented in Table 1.

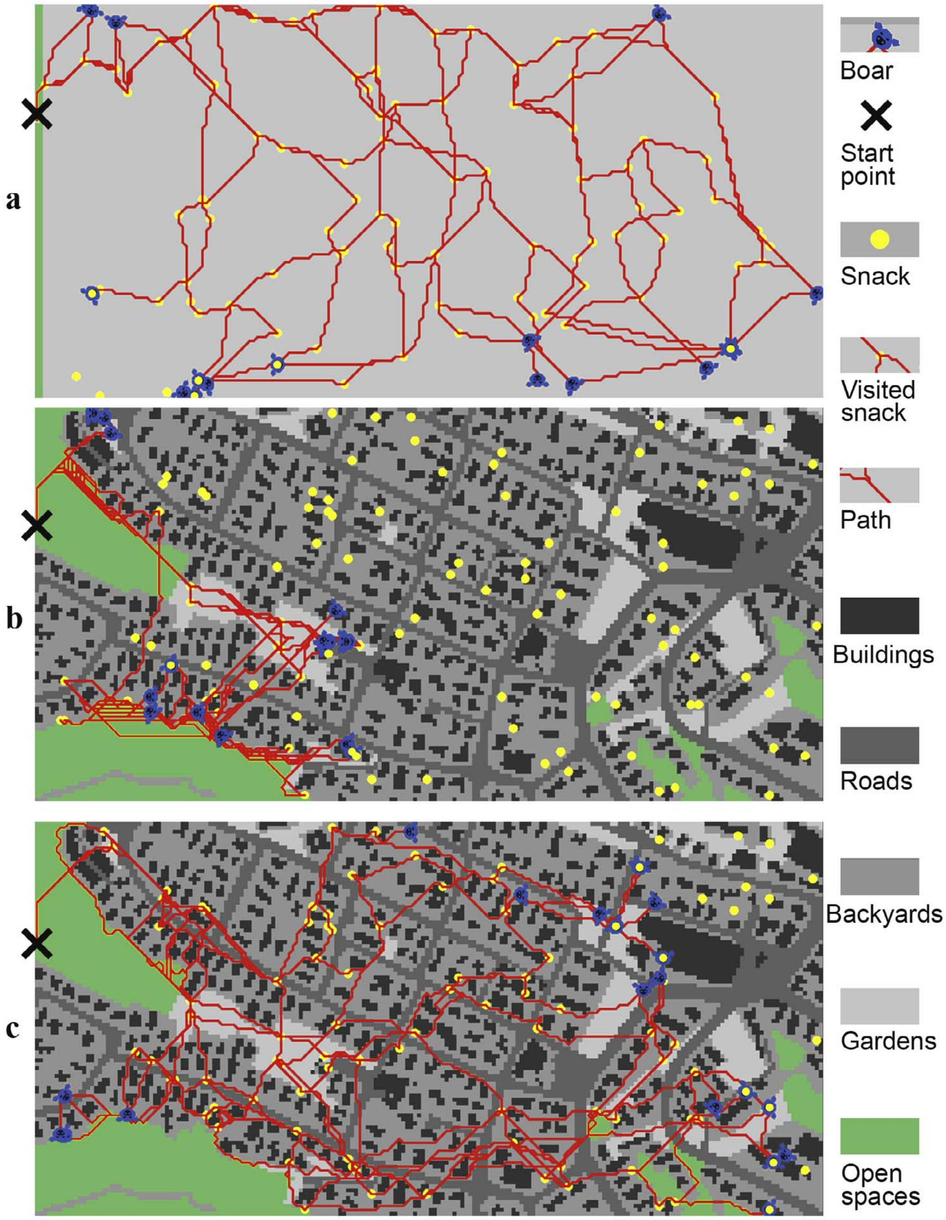


Fig. 6. Simulated trajectories of 10 boars during the night for *SPB* = 5. (a) *Garden*, $\gamma = 0.3$/m; (b) *Haifa1*, $\gamma = 0.3$/m and (c) *Haifa2*, $\gamma = 0.6$/m.

2.6. Formalization of boars' movement

After a boar selects a target snack *i*, the least-cost path is established between the boar's current location and snack *i*, and the average cost γ of traversing a cell along the path is calculated. If γ is higher than γ_{max}, the path is excluded from consideration. We consider this approach as an outcome of a simplified memory-based trial and error process. Namely, the boar remembers previous attempts to traverse the area and avoids paths that contain too many costly cells.

On the way to a selected snack, at each cell, the boar might re-evaluate the attractiveness of targets that it can smell and decide to move to a target of higher attractiveness. Below, we apply the probability of re-evaluation $p_{reevaluaiton} = 0.1$.

2.7. Model scenarios

We investigated boars' movement in three contexts, an abstract uniform *Garden* space, a real *Haifa* landscape (Fig. 1), and a generalized synthetic landscape that reflects average Haifa landscape (Table 2). The Garden scenario represents a situation where the boars have no obstructions and even with low tolerance to human activities should be able to infiltrate easily far into the city. Hence we set $\gamma = 0.25$ for every cell and $\gamma_{max} = 0.3$. Haifa scenarios represent low and high levels of obstruction to the boars' movement and, respectively, are investigated for low and high values of $\gamma_{max} = 0.3$ (*Haifa1*) and $\gamma_{max} = 0.6$ (*Haifa2*). The synthetic landscape was used for comparison of the model outputs and Haifa observations. Thus we estimated frequencies of the nightly visits to Haifa at different distances from the city fringe for varying values of γ_{max} and compare these distributions to the observed ones (see below). In a homogeneous Garden, the snacks are randomly allocated over the entire area, while in Haifa and synthetic landscapes, snacks are randomly allocated in the cells of the backyard LULC type.

The models begin with ten boars start at the boundary between the open space and the urban area. We investigated each model type for two initial distributions of boars in space: all boars at the same location and random allocation of boars along the border, and for three values of the threshold distance at which the boars can detect a snack (smell range), 250 m, 500 m, and 1000 m. The results do not depend on the

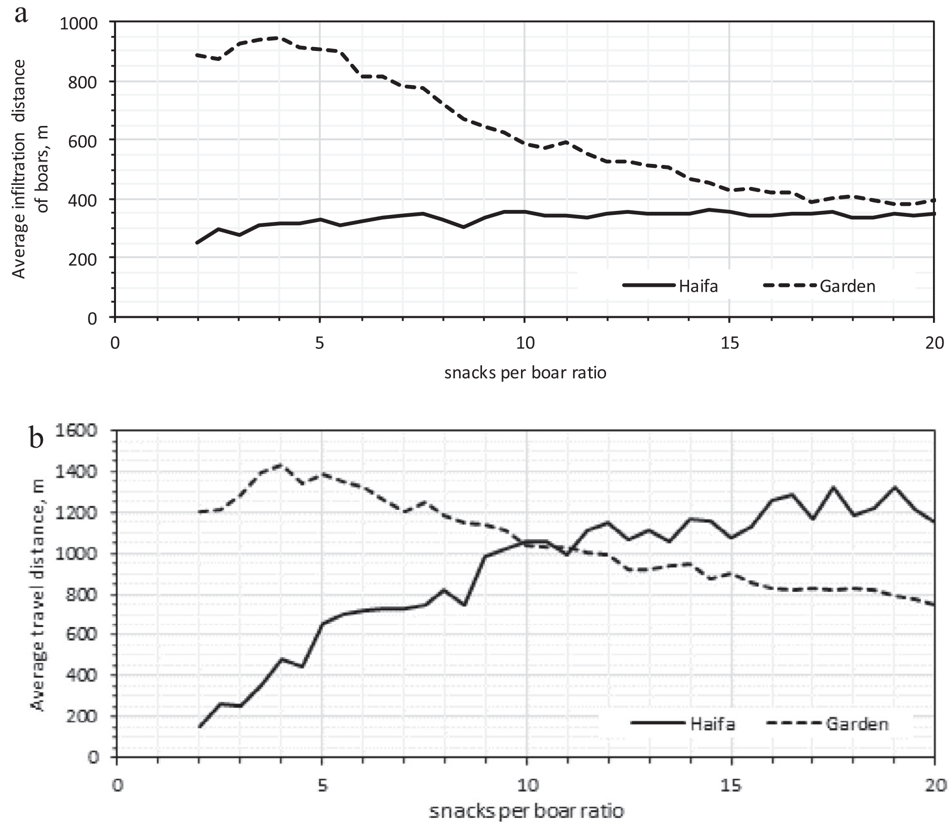


Fig. 7. A comparison of the *Haifa1* and an abstract *Garden* scenario as dependent on SPB (γ_{max} = 0.3/m in both cases): (a) distance infiltrated into the city, and (b) total traveled distance averaged by boars. Note the different value scales of the y-axis.

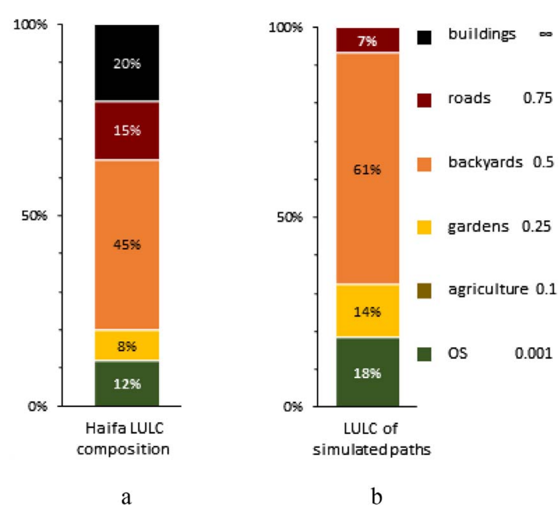


Fig. 8. A comparison of the LULC composition in (a) *Haifa1* and *Haifa2* scenario landscapes setting and (b) along the boars' paths in *Haifa2* scenario, γ_{max} = 0.6.

initial spatial distribution of boars and on the smell range, thus we present the results obtained for the common initial location and smell-range of 500 m.

In each scenario, we distribute N_{snacks} snacks representing human-generated food sources such as garbage bins, cat feeding points, compost, and fruit and seeds from garden plants. Each snack initially contains 60 units of food sufficient for a 1-h feed of a boar. To investigate the influence of the food density, we vary the number of Snacks-Per-Boar (*SPB*) between 2 and 20. For each set of parameters, we repeat simulation 10 times and present averages values of model's characteristics.

2.8. Wild boar observations in Haifa and estimation of boars' abundance

Haifa municipality systematically records wild boars' observations reported by citizens. The number of calls increased from 1322 (2011) to 2004 (2013) calls per year (Fig. 3). The distribution of distances from the point of boar's observation to the nearest border of the buildup area, estimated as a distance (m) to the nearest green space that is larger than 3 ha (Fig. 3d), shows that boars infiltrate up to ca. 450 m into the city. The deep infiltration, coupled with the growing number of observations, explains increasing concern of Haifa citizens and municipality. We assume that the number of boar sightings in the area is proportional to the boars' abundance and human population density of the area, the latter available from the population census data (CBS, 2009). We thus estimate boars' abundance (Fig. 4c) as a number of the sightings (Fig. 4a) per 1000 residents of the area (Fig. 4b).

To validate the model, we use the D-measure employed in the Kolmogorov-Smirnov statistic (Kraska-Miller, 2013). Based on the data presented in Fig. 4, we estimate the accumulated fractions of boars O_d observed at a distances d less or equal than 50, 100, 150, … 500 m from the boundary of the open space (Fig. 5), and compare them to same fractions S_d estimated from the simulations. D is the maximal, over distances, absolute difference between these fractions: $D = \max_d |O_d - S_d|$.

3. Results

3.1. The boars' infiltration into the city as dependent on the amount of available food

In the homogeneous *Garden* landscape with γ = 0.25 for every cell, γ_{max} = 0.3 is never achieved and boars' locations during the night form a front that extends towards the distant boundary of the investigated

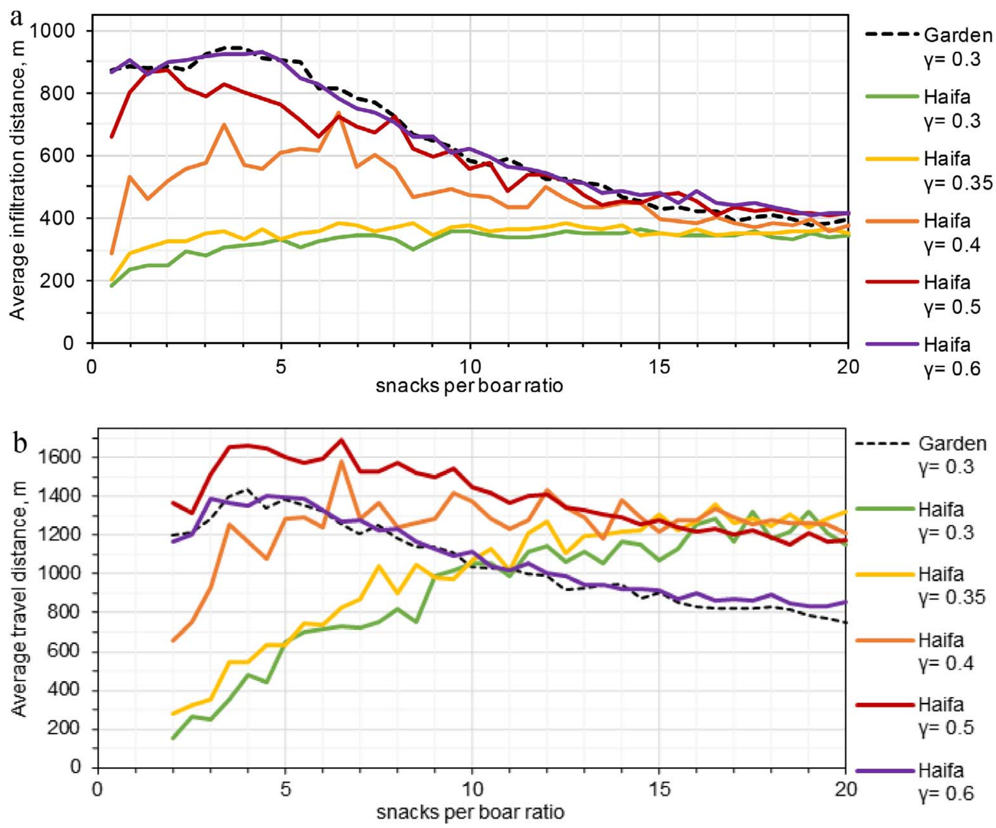


Fig. 9. (a) Average infiltration and (b) total travel distance of boars as dependent on γ_{max} in Haifa scenarios.

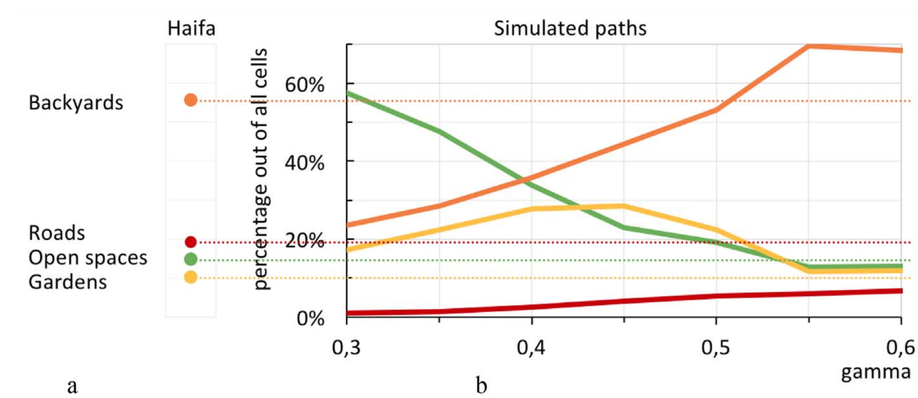


Fig. 10. (a) LULC composition (without non-traversable buildings) of the *Haifa* scenarios landscape; (b) dependence of LULC types along boars' simulated paths in these scenarios, as dependent on γ_{max}.

area (Fig. 6a). In heterogeneous *Haifa1* and the same $\gamma_{max} = 0.3$, the average cost of *any* path between most of the snack pairs is above the threshold and, thus, boars remain close to the natural areas at the city boundary during the entire night (Fig. 6b). The situation changes for the scenario *Haifa2* when γ_{max} is increased to 0.6/m (Fig. 6c) in that the boars infiltrate Haifa much deeper, just as far as in the homogeneous *Garden* landscape.

The effects of the density and amount of food are different in the homogeneous and heterogeneous landscapes (Fig. 7). In the homogeneous *Garden* landscape, with the increase in SPB, the density of snacks becomes high enough for feeding close to the boundary of the area most of the time and the infiltration distance decreases (Fig. 7a). At the same time, the increase in amount of food results in the decrease of the boar's travel distance (Fig. 7b). In *Haifa1* scenario case, $\gamma_{max} = 0.3$/m restricts boars' movements irrespective of the SPB (i.e. their paths cannot avoid costly backyards and roads). As a result, the boars remain locked close to the boundary, where the share of open spaces and gardens is high and with the increase in SPB, the infiltration distance into Haifa only slightly increases (Fig. 7a). In the same time, the average traveled distance grows proportionally to the SPB as the number of points over the entire accessible area where they can feed increases (Fig. 7b). Note that the absolute infiltration distance in *Haifa1* scenario with $\gamma_{max} = 0.3$/m is about 350 m, 100 m lower than the distance observed in reality (Fig. 3). We consider this as an argument in favor of the traverse threshold γ_{max} being higher than 0.3/m in real Haifa.

3.2. The boars' infiltration into the city as dependent on the traverse threshold γ_{max}

The influence of the traverse threshold (γ_{max}) on the model outcome is defined by LULC composition along the paths chosen by boars. Boars

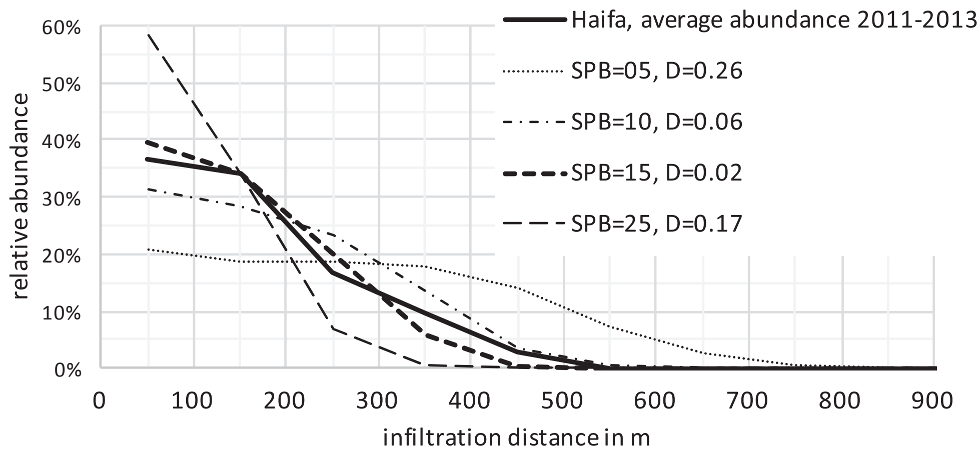


Fig. 11. Observed and simulated boars' abundance as dependent on the distance from the open space and the values of D-statistics.

prefer open spaces and gardens and land composition along the chosen paths (Fig. 8b) contains essentially higher fraction of traversable LULC types (Fig. 8a).

The boars' ability to traverse Haifa urban space is strongly dependent on γ_{max} (Fig. 9). For low γ_{max} ($\gamma_{max} < 0.4$/m), Haifa remains impenetrable for the boars. For the $\gamma_{max} > 0.4$/m, the Haifa landscape becomes increasingly porous for the boars and starting from $\gamma_{max} \sim 0.55$/m the Haifa landscape does not restrict boars' movements (Fig. 9). Moreover, the dependence of the infiltration distance and travel distance on the amount of food (expressed by the SPB) in Haifa scenario becomes, for $\gamma_{max} > 0.55$, the same as in the homogeneous *Garden* case. In the same way, for relatively low γ_{max} total travel distance grows with the increase in SPB, but when the landscape becomes fully traversable with increase in γ_{max}, average travel distance decreases with the increase of SPB, similar to fully traversable homogeneous *Garden* landscape. Different from the homogeneous *Garden* scenario, where boars' paths cover the entire area, boars' paths to the food sources in *Haifa* scenarios for high γ_{max} follow the inexpensive vegetated gullies and backyards, which fraction along the simulation paths steadily grows with the growth of γ_{max}, stabilizing at $\gamma_{max} \sim 0.55$ (Fig. 10).

3.3. Model results versus the data on boars' infiltration into Haifa

To validate our model qualitatively, we compared the outcomes obtained for the *Synthetic* Haifa landscape (Table 2) to the observed boars' abundance in Haifa (Fig. 5). To account for the dependence of model outcomes on the density of food, we compare Haifa data to the model outcomes for different values of the SPB. The model output for the SPB = 15 fits best to the Haifa data (Fig. 11) with the value of D = 0.02. For the lower SPB, model boars move too far into Haifa, while for the higher SPB they remain closer to the border of the buildup area. We thus consider SPB = 15 as reflecting the state of Haifa with food being abundant enough to facilitate entering the city, but not so ubiquitous to the point where there is no need to go far.

4. Discussion and conclusions

Our model highlights key drivers that might explain why and how wild animals traverse urban landscapes. We demonstrated that cityscapes such as Haifa provide a network that makes food accessible and that heterogeneity of Haifa land cover is sufficient for the boars to circumvent the obstacles and develop traverse routes that take them far into the buildup area. The simulations indicated that abundant shortcuts via wadis, open areas and vegetated backyards make Haifa penetrable to boars. In other cities, riverbeds and other open spaces can provide the connecting functions, as, for example, in Hannover, where the proportion of open spaces is similar to that in Haifa (Matthies et al., 2013).

In a porous city, the distance of boars' infiltration depends on relative availability of food – the SPB ratio. Given the fixed extent of the model, we can generalize this ratio as Snacks-per-Boar-per-Area. The dependence of the infiltration distance on the SPB is non-linear and defined by the total travel distance that boars cover during the night to accumulate the required amount of food. When SPB is low, boars cannot find the next snack to feed after exploiting the current one and may cover large distance searching for food. When the SPB ratio increases, the necessary amount of food can be accumulated over a smaller area and the infiltration depth decreases. Note that in our model, the boar population is static. But, it is reasonable to assume that in the long run the abundance of food and urban porosity may cause the boar population to grow.

Our model presents results in the case of a specific urban morphology of the city of Haifa. Other cities have different patterns of roads and buildings, gardens and open spaces. To extrapolate model results, we utilize γ_{max} – a penetrability index that characterizes urban landscape along possible movement paths. It is a valuable method for studying animal movement ecology in urbanized areas. The value of γ_{max} is defined by the LULC types that are exploited by the mammal species for movement between the food attractors. The entire LULC pattern and not the ratio of the LULC only is critical in this respect and different patterns of the food sources may entail easy or conversely, complex paths that demand crossing dangerous patches. The value of γ_{max} shapes the model dynamics – when γ_{max} is low, animals remain within the areas near the border of the buildup area, when it is high, the entire pattern of the food sources in the city becomes important. We consider wild boars an opportunistic species that has high γ_{max} and assume that for the local boar population that regularly feeds in the city, the value of γ_{max} may grow over time, when individuals become habituated to human activities.

Representation of food sources as a set of snacks, each replenished anew every day, limits non-urban applications of our model. Natural food sources are less concentrated, have different temporal dynamics and replenish gradually, and thus cannot be considered as a simple network such as implemented here. Our model assumes that boars know the least-cost paths between the food sources. In reality, these paths are established by multiple trial and error experiments, using memory, scent marks or both. Empirical studies of wild and domesticated pigs foraging behavior indeed suggest memory-related exploration of territory and returning to known food locations (Gustafsson, Jensen, de Jonge, & Schuurman, 1999). In accordance to the Lévy flight foraging movements (Viswanathan, Raposo, & Luz, 2008), experiments showed faithfulness to certain areas combined with rare sallies over larger ranges, supporting incorporation of boars' ability to memorize paths into the model and thus exploring the emergence of paths between food sources in the city. We plan to investigate these memory-based assumptions in our future studies.

Haifa data collected since 2010 indicate increasing wild boars' infiltration into urban areas, and the policy makers seek ways to minimize the damages from wild boar overabundance and reduce human-wildlife interactions. Haifa is not unique in this respect. Concern over the presence of wild boars in cities is an example of concern for wildlife issues for other species. Haifa municipality's attempts to decrease wild boar abundance in the city by culling (JPost.com, 2007) and the educational campaign against intentional feeding (Yaron, 2014) sparked considerable public opposition. This motivates the search for alternative policies, such as boar-proofing garbage bins or fencing against boar infiltration. Licoppe et al. (2013) surveyed the mitigation policies applied in various cities and their research confirm that the costs and benefits of alternate decisions, such as reduction in boar population or available food sources, should be evaluated in terms of the dynamics of entire system as it is considered in our model. Using our modeling framework, policies can be categorized as targeting one or more of the variables that impact boars' infiltration: population size, availability and spatial distribution of resources, friction of the landscape to movement along potential movement paths, and habituation of the wildlife to urban environment.

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