Limiting factors of Striped Hyaena, *Hyaena hyaena*, distribution and densities across climatic and geographical gradients (Mammalia: Carnivora)

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Few previous studies on the factors that affect Striped Hyaena (*Hyaena hyaena* Linnaeus, 1758) occurrence and densities were done on geographically unrelated populations using different methodologies. In Israel, hyaenas occur throughout the country’s steep climatic and geographical gradients, presenting a unique opportunity to study densities and habitat use across adjacent ecosystems using a unified methodology and test previous conceptions regarding the species’ habitat selection. We collected hyaena abundance-absence data using 1440 camera traps placed at 80 sites (2012–2016). Site location ranged from hyper-arid deserts to dense Mediterranean shrubland.

We assessed the effect of climate, habitat structure, elevation, geomorphological attributes (proxy for den availability), and anthropogenic development (proximity to settlements and agriculture) on hyaena densities using N-mixture models. Hyaena densities were negatively affected by anthropogenic development, and were limited by den availability. Hyaena densities did not follow a climatic or geographic gradient. Densities were highest at hyper-arid deserts and Mediterranean coastal shrublands. Despite the former conception that hyaenas prefer semi-arid open habitats and avoid extreme deserts and dense vegetation, we show that hyaenas use and even thrive in these habitats when geomorphological conditions are suitable and resources are available.

**Keywords:** N-mixture models; population density; habitat selection, camera traps

Introduction

The Striped Hyaena (*Hyaena hyaena* Linnaeus, 1758) is a large elusive carnivore and much is still unknown about their ecology. In Israel, the Striped Hyaena is distributed across the country’s variable geographical and steep climatic gradients. This presents a unique opportunity to assess the limiting factors for its habitat use and limiting factors of spatial distribution across adjacent ecosystems. Few local short-term studies on unrelated populations from different regions throughout Striped Hyaena geographic distribution were carried out, using different methodologies such as indirect sightings and field signs (tracks and scats) (Abi-Said & Abi-Said, 2007; Reichmann, 2005), movement data (Reichmann, 2005; Rosenberg, Reichman, & Shamoon, 2016; Van Aarde, Skinner, Knight, & Skinner, 1998; Wagner, Frank, & Creel, 2008) and camera traps (Abi-Said & Amr, 2012; Akay, Inac, & Yildirim, 2011; Alam, Khan, & Pathak, 2015; Rosenberg et al., 2016; Singh, Gopalaswamy, & Karanth, 2010; Tichon, Rotem, & Ward, 2016). The use of different methodologies makes it difficult to compare results among studies or compare habitat selection across ecosystems.
The distribution of the Striped Hyaena extends from north and northeast Africa through the Middle East and central Asia including India. The species occupies varied types of environments and ecosystems (Akay et al., 2011; Reichmann, 2005), extending from arid deserts (Singh et al., 2010; Tichon et al., 2016; Wagner, 2006) to dense Mediterranean shrubland (Abi-Said & Abi-Said, 2007; Rosenberg et al., 2016). It was reported that hyaenas prefer open semi-arid habitats (Alam et al., 2015; Wagner, 2006), and occur in low densities in true deserts and dense vegetation (Abisaid & Dloniak, 2015). Striped Hyaenas rely on large areas to support their resource requirements (Alam et al., 2015; Wagner, 2006). Average home-range size is known to vary between ~40 km² and ~100 km² (home-range based on radio telemetry ranges between 44 and 72 km² in the Serengeti, Tanzania; 60 km² in the Negev Desert, Israel; 95 km² in Mediterranean shrubland, Israel; 62–76 km² in Loisaba savanna, Kenya (Tichon et al., 2016; Wagner et al., 2008)). Hyaena population densities also vary across their distribution, ranging between 1.5 and 8.5 individuals/100 km² (Alam et al., 2015; Singh et al., 2010; Singh, Qureshi, Sankar, Krausman, Goyal, & Nicholson, 2014; Tichon et al., 2016).
While the Striped Hyaena is characterised as solitary (Abisaid & Dloniak, 2015), some studies report that the species forms groups and may share living space. Macdonald (1978) was the first to report different social organisation of the species in Israel, noting that hyaenas occurring in Israel were “less strictly solitary” in comparison to their East African counterparts. A more recent study reported that a Kenyan population form stable, spatially associated groups composed of one adult female and up to three adult males (Wagner, 2006). Similar findings have been reported from Israel since (Rosenberg et al., 2016), however with different group organisation of one male and up to four females sharing a living space. In Lebanon, a survey using pre-baited camera traps reported that Striped Hyaenas form small groups ranging from 3 to 9 individuals of adults and juveniles (Abi-Said & Amr, 2012). These findings have changed perspective on Striped Hyaena ecology and biology, emphasising the need to re-estimate population densities in different habitats, especially in areas where indirect observations such as tracks and scats were previously used for such calculations with the old notion of strictly solitary behaviour (Abi-Said & Abi-Said, 2007; Reichmann, 2005).

Previous studies suggested that hyaena densities are limited by three main factors: 1) Habitat availability: affected by anthropogenic development (i.e. habitat loss) and anthropogenic activity, i.e. persecution (Abisaid & Dloniak, 2015; Kasparek, Kasparek, Gözcelioğlu, Çolak, & Yiğit, 2004; Tourani, Moqanaki, & Kiabi, 2012); 2) habitat quality and resource availability: Striped Hyaenas are primarily scavengers (Wagner, 2006) and rely on opportunistic food resources. The species is relatively well adapted to dry habitats but need a water resource within 10 km in such habitats (Wagner, 2006); 3) den availability (Singh et al., 2010).

In the current study, we assessed hyaena densities across Israel’s geographic and climatic gradients, and assessed the importance of hyaena limiting factors. Hyaenas’ camera trap detections were sampled in different ecosystems ranging from hyper-arid desert to dense Mediterranean shrubland and herbaceous steppe. We used systematic and unified methodologies, both spatially and temporally, allowing us to determine the factors limiting the distribution of the Striped Hyaena in relation to climate, proximity to anthropogenic development, topography, geomorphology and habitat quality.

Methods

Study area. Data used for this study is part of Israel’s National Biodiversity Monitoring Program run by HaMaarag – Israel’s National Nature Assessment Program (www.hamaarag.org.il). Within this framework, large mammals are monitored throughout Israel using camera traps across 10 habitats, each unique in terms of climate, vegetation structure, vegetation productivity, and degree of anthropogenic development. Ranging from south to north (Figure 1):

Hyper-arid lowland desert (Arava Valley) is characterised by extreme low annual precipitation (<30 mm) and an average summer temperature of 31°C. The area remains dry most year round except ephemeral streams that flood briefly after sporadic and uncommon rain events during winters. The most stable biomass producers in the desert resource web are trees belonging to the genus *Acacia* which are considered key stone species (Danin, 1986). Anthropogenic resources such as landfills or disposed livestock carcasses can be found in proximity to human settlements, and agricultural fields, mainly disposed livestock carcasses. The regional bed rock consists mainly of limestone and dolomite, and sand and silt soil (Arkin, Ichoku, & Karnieli, 1999).

Arid highland desert (Negev Highlands) is a mountainous a rocky terrain characterised by low annual precipitation of ~80 mm and mean summer temperature of 26°C. Several ephemeral streams drain after sporadic rain events either northwest to the Mediterranean and northeast to the Dead Sea basin. Regional bedrock consists mainly of marine sediments (limestone, dolomite, chalk and chert) (Avni, Porat, Plakht, & Avni, 2006). Dominant shrub cover (5-15%, 40 cm height) consists of *Artemisia sieberi* and *Gymnocarpus decanter* (Kidron, Yair, & Danin, 2006).
and annual vegetation cover ranges between 5 and 50% during winter and spring depending on slope, bedcover and precipitation (Ayal & Merkl, 1994).

**Arid steppe** area is a transitional landscape that connects Mediterranean region, Judea desert and Negev desert (Schmidt & Gitelson, 2000). Mean annual precipitation ranges between 150 and 300 mm. Mean summer temperature is ~25°C. Vegetation cover mainly consists of typical Irano-Turanian region shrubs (<30% cover) and annual grass (30–60%). The regional bedrock consists mainly of limestone hills surrounded by loessial valleys (Rotem, Ziv, Giladi, & Bouskila, 2013). Large natural areas in the region were altered to agriculture or are under heavy livestock grazing.

**Mediterranean highland shrubland** (Judea Highlands) is a mountainous area characterised by mean annual precipitation of 350–500 mm and mean summer temperature of 28°C. Vegetation is evergreen Mediterranean shrub, with scerophyllous trees, mainly *Quercus calliprinos*, *Ceratonia silique*, *Calicotome villosa*, *Rhamnus lycioides*, *Phillyrea latifolia*, and *Cistus* sp. Bedrock consists of limestone, chalk and marl, and dolomite. Small farming villages are found on the border of woodland and shrub areas.

**Coastal Mediterranean shrubland** (Mt. Carmel) is a mountainous area characterised by mean annual precipitation of 500–600 mm and mean summer temperature of 27°C. Dense vegetation of woodland and shrub cover most of the natural area and consists mainly of *Ceratonia silique*, *Pistacia lentiscus*, *P. palaestina*, *Rhamnus lycioides*, *Phillyrea latifolia*, and *Quercus calliprinos*. Coastal Mediterranean bedrock consists of marine sediments (chalk and limestone; chalk and marl; clay, silt, sand and gravel [alluvium soil]; igneous and metamorphic; limestone chalk and marl; limestone and dolomite). The lithological and topographic characteristics contribute to karst collapse due to climate conditions near the coast (Barnes & Worden, 1998; Weinstein-Evron et al., 2012). Small farming villages are embedded within woodland and shrubland.

**Inland Mediterranean shrubland** (Galilee Mts.) is a mountainous area characterised by mean annual precipitation of 500–800 mm and mean summer temperature of 29°C. Dense woodland and shrub vegetation consist mainly of *Pistacia palaestina*, *Quercus calliprinos*, *Rhamnus lycioides*, *Phillyrea latifolia*. Small farming villages are embedded within woodland and shrub.

**Planted conifer forests** that occur in the three Mediterranean ecological units (highland; coast; inland) are made up of *Pinus halepensis* trees. We sampled in planted forests that were 40–60 years old. These forests can be found in all three Mediterranean ecozones stated above and therefore were considered as three forest habitat types accordingly. Climate and bedrock attributes are the same as Mediterranean shrub ecozones (described above).

**Northern steppe** (Golan Heights) is characterised by mean annual precipitation of 400–650 mm and mean summer temperature of 29°C. Bedrock is mainly basalt with occasional sand stones on the surface (Noy-Meir, 1995). Vegetation cover is characterised by low (<20%) shrub cover and seasonal grass with Irano-Turanian elements together with predominant Mediterranean species (Neumann, Schölzel, Litt, Hense, & Stein, 2007). Most open areas are grazed by cattle. Agriculture fields and orchards, as well as poultry farms are found around human settlements.

**Camera trap design.** We used infra-red (IR) camera traps (Reconyx HC500, USA) to assess Striped Hyena distribution and population densities during two monitoring cycles (springs of 2013–2014 and 2015–2016). The Mediterranean region was divided into three ecozones because of substantial differences in climate, bedrock and vegetation. We assessed the effects of habitat type, vegetation productivity measured by Normalized Difference Vegetation Index (NDVI), mean annual precipitation, altitude, lithological characteristics (proxy for den availability), and proximity to anthropogenic development (settlements and agriculture). The latter is divided to two categories: 1) near anthropogenic development (<100 m); 2) far from anthropogenic development (>750 m). At each site, we set nine cameras with ~85 m intervals between them. Cameras were set 50–70 cm above ground level at 45° angle toward a natural animal trail. Cameras trigger was set to zero seconds, and five images in each burst. A single detection was considered as the sequence of images of the same individual within a window of 5 minutes. Cameras were set in the field for 10 consecutive days. We collected data from a total of 720 cameras in 80 transects per monitoring cycle. Data was collected twice in each site (e.g. two cycles: spring of 2013–2014 and spring 2015–2016) resulting in over 14,000 camera days throughout the study period. Images
were sorted and identified to the species level. The data were collected by Hammarag, Israel’s National Nature Assessment Program.

**Statistical analysis.** We estimated Striped Hyaena densities using N-mixture models (Royle, 2004). N-mixture models are hierarchical models made up of one sub-model that estimates detection probability (i.e. correcting for type II error), and a function that estimates the spatial and temporal variation in latent states. It is used to estimate population size/density from spatially and temporally replicated counts of unmarked animals, while accounting for imperfect detection (Joseph, Elkin, Martin, & Possingham, 2009; Royle, 2004). We used the ‘unmarked’ package (Fiske & Chandler, 2011) on R (R Core Team, 2015) to analyse our data. Data collected in this program can be accessed through Global Biodiversity Information Facility (GBIF) repository (www.gbif.org/publisher/d311f0e2-e067-4df9-9374-ae058ea4c19f).

**Spatial covariates.** Hyaena distribution and population densities were tested in relation to three possible limiting factors: proximity to anthropogenic development, habitat productivity, and den availability.

**Anthropogenic development.** We tested the effect of proximity to anthropogenic development (settlements and agriculture) in relation to hyaena spatial activity.

**Habitat quality and resource abundance** We used NDVI, a measurement of available energy in a system, as a surrogate for resource abundance and habitat quality (Krishnaswamy, Bawa, Ganeshiah, & Kiran, 2009; Phillips, Hansen, & Flather, 2008). The available energy in a given system is correlated to biological diversity (Oindo & Skidmore, 2002; Somveille, Rodrigues, & Manica, 2018), and can reflect on availability and abundance of resources for a given species (Somveille et al., 2018; Youngentob, Yoon, Stein, Lindenmayer, & Held, 2015). NDVI calculation was based on Moderate Resolution Imaging Spectroradiometer (MODIS) 250 m resolution (16 day interval data) obtained from National Aeronautics and Space Administration (NASA) TERRA and AQUA satellites.

**Den availability.** Geomorphology features (i.e. type/number of lithological layers) can be used to predict cave/den availability (Heydari, 2007; Rauch & White, 1970). We assessed den availability by using a lithological characteristics layer obtained from Sneh and Rosenhaft (2014). Each rock type was assigned one of two categories: hard rock (basalt, limestone and dolomite) and soft rock/soil (gravel, sand, clay, chalk). Stable dens may be more easily maintained in areas where both hard and soft rock occur. Hard rock form the foundation, whereas soft rock is easily dug up. We assumed that den availability will be directly tied to lithological characteristics and may further explain hyaena densities throughout Israel. The number of exposed layer types (hard or soft) around each sampled plot were counted within a 5 km buffer. Dens are dug up in the transitions between these rock/soil layers. The number of hard/soft exposed layers were used as proxy for den availability in hyaena density estimation models. We hypothesis that the more layers exposed, and the greater the mixture between foundation rock and soft rock, will increase the chance for suitable conditions for dens.

**Habitat type.** Ten habitats (see study area) were simplified by vegetation structure into four main habitat types (see Figure 1): Arid desert (hyper-arid lowland desert, arid highland desert), steppe (arid steppe and northern steppe), Mediterranean shrubland (inland, coastal, and highland shrubland) and conifer forests (inland, coastal, and highland shrubland).

**Elevation.** Digital Elevation Model (DEM) were obtained from Landsat Level-1 satellite 30m resolution (https://landsat.usgs.gov).

Mean annual precipitation and mean annual temperature were ranked lower than the null model and therefore are not presented in this article results.

**Results**

We recorded 246 independent encounters of Striped Hyaena during the study period. Out of these, 174 encounters were recorded away (>750 m) from anthropogenic development and 72 near (<100 m) anthropogenic development. Multi-model selection revealed that proximity to anthropogenic development (settlements and/or agricultural
Table 1. Multi-model selection ranked by Akaike information criterion (AIC). Model covariates: Habitat type (Arid desert (intercept); Steppe; Shrub-land; Conifer Plantations); Lithology – number of lithology layers characterised as soft or hard layers within a 1 km buffer; Normalized Difference Vegetation Index (NDVI); Proximity – far (over 750 m from anthropogenic development) (intercept), near (up to 100 m) anthropogenic develop-ment.

| Model No. | Model                                      | negLog Like | nPars | AIC    | delta | AICwt | cumlt-vWt |
|-----------|--------------------------------------------|-------------|-------|--------|-------|-------|----------|
| 1         | Habitat type + Soft * Hard + Proximity + DEM| 913.48      | 11    | 1848.97| 0.00  | 0.80  | 0.80     |
| 2         | Number.of.layers + NDVI + Proximity + DEM  | 919.90      | 7     | 1853.81| 4.84  | 0.07  | 0.88     |
| 3         | Habitat type + NDVI + NDVI² + Soft * Hard + Proximity + DEM | 913.94      | 13    | 1853.88| 4.92  | 0.07  | 0.94     |
| 4         | NDVI + I(NDVI²) + Soft * Hard + Proximity + DEM | 917.95      | 10    | 1855.91| 6.94  | 0.03  | 0.97     |
| 5         | Habitat type + NDVI + NDVI² + Soft + Hard + Proximity | 917.05      | 11    | 1856.10| 7.14  | 0.02  | 0.99     |
| 6         | Habitat type + Soft * Hard + Proximity    | 919.63      | 10    | 1859.26| 10.29 | 0.00  | 1.00     |
| 7         | Habitat type + Proximity + Number of layers | 922.04      | 8     | 1860.07| 11.11 | 0.00  | 1.00     |
| 8         | NDVI + NDVI² + Proximity + Soft * Hard    | 922.56      | 9     | 1863.12| 14.15 | 0.00  | 1.00     |
| 9         | Habitat type + Proximity                  | 944.23      | 7     | 1902.46| 53.49 | 0.00  | 1.00     |
| 10        | Habitat type                              | 948.60      | 6     | 1909.20| 60.23 | 0.00  | 1.00     |
| 11        | NDVI + NDVI²                               | 953.89      | 5     | 1917.79| 68.82 | 0.00  | 1.00     |
| 12        | Intercept only                            | 1138.34     | 2     | 2280.67| 431.71| 0.00  | 1.00     |
Table 2. Top model density estimation in ten habitats across Israel’s climate and habitat gradient. Model covariate: Habitat type + Soft × Hard + Proximity + DEM. Estimation presented by proximity categories: near anthropogenic development (up to 100 m), away from anthropogenic development (over 750 m from anthropogenic development).

| Habitat                          | Proximity to anthropogenic development | Density estimation / average homerange |
|---------------------------------|---------------------------------------|---------------------------------------|
| Hyper arid lowland desert       | >750m                                  | 3.57±1.38                             |
|                                 | <100m                                  | 2.36±1.22                             |
| Arid highlands desert           | >750m                                  | 3.71±1.73                             |
|                                 | <100m                                  | 2.35±1.37                             |
| Arid steppe                     | >750m                                  | 0.91±0.88                             |
|                                 | <100m                                  | 0.53±0.15                             |
| Mediterranean highlands shrubland | >750m                                  | 1.39±0.52                             |
|                                 | <100m                                  | 0.92±0.34                             |
| Mediterranean forest            | >750m                                  | 1.97±1.01                             |
| Mediterranean coast shrubland   | >750m                                  | 4.47±1.29                             |
|                                 | <100m                                  | 2.79±0.93                             |
| Mediterranean coast forest      | >750m                                  | 3.33±1.15                             |
| Inland Mediterranean shrubland  | >750m                                  | 0.21±0.12                             |
|                                 | <100m                                  | 0.12±0.07                             |
| Inland Mediterranean forest     | >750m                                  | 0.26±0.10                             |
| Northern steppe                 | >750m                                  | 0.44±0.36                             |

fields), elevation, habitat type and lithological characteristics had the greatest effect on hyaena densities (Table 1). Hyaena were negatively affected by proximity to anthropogenic development (βhuman: -0.495±0.231) and negligibly affected by elevation (βDEM: -0.007±0.002) (Supplementary Table 1).

Hyaena density estimates did not follow the climate gradient (north to south). Vegetation productivity measured by NDVI did not affect hyaena densities. The density estimates in Mediterranean shrubland near the coast were not significantly different from arid habitats (used as intercept) (βshrubland: -0.029±0.37) (Table 2). Densities were recorded in conifer plantations and steppe (βconifer: -2.669±0.93; βsteppe -0.204±0.10) were significantly lower that arid habitats and coastal Mediterranean shrublands (Supplementary Table S1).

Lithological characteristics in each habitat type had significant effects on hyaena densities, primarily through interaction between the number of soft and hard rock layers in each sampled site (βhard-soft: 0.388±0.19) (Supplementary Table 1). Lithological characteristics contributed to variation of density estimates throughout the Mediterranean region (both shrubland and conifer forest habitats). We sampled three Mediterranean landscapes (highland coast, semi-dry highlands and inland). We found hyaena densities in highland coastal areas to be approximately three-folds higher than semi-dry Mediterranean inland highlands, and over 20-folds higher than inland Mediterranean highlands (Table 2). Similar and slightly lower densities than coastal highland Mediterranean shrubland were calculated at highlands arid desert and hyper-arid desert units. Extreme low densities were estimated in the northern units (Mediterranean conifer forest, and steppe) (Table 2).
Table 3. Comparison of N-mixture density estimates to previous studies on Striped Hyena density in three units. 

| Unit             | Sources                  | Density per km² | N-mix per km² | HR in km² |
|------------------|--------------------------|-----------------|---------------|-----------|
| North region     | Abi-Said 2006, Lebanon   | 0.01            | 0.0021        | 100       |
| North region     | Reichman 2005            | 0.016           | 0.0044        | 98        |
| Coastal shrubland| Rosenberg et al. 2016    | 0.050           | 0.0447        | Unknown, assumed 100 |
| Semi-arid steppe | Shamoon et al. 2018      | 0.013           | 0.0091        | 100       |
| Arid Highlands   | Van Aarde et al. 1998    | 0.016           | 0.0618        | 60        |
| Arid Highlands   | Tichon et al. 2016       | 0.018           | 0.0618        | 60        |

Discussion

Striped hyaena population densities were limited by geomorphological attributes, habitat type, and proximity to anthropogenic developments. Our results suggest hyaena densities are higher away from humans’ settlements and agriculture. That is not to say hyaena do not occur near human habitation, but rather that densities are higher away from humans. We also found that Striped Hyena densities do not follow a geographical and climatic gradient and were higher in arid deserts and in Mediterranean shrubland habitats. Striped hyaena mostly occur in arid open steppe and shrub habitats throughout their distribution and avoid true deserts (Abisaid & Dloniak, 2015). Despite previous conceptions that Striped Hyena avoid dense vegetation, there are reports that Striped Hyena occur in dense oak forests (Abisaid & Dloniak, 2015), however many areas lack density estimates. Our findings not only support that Striped Hyena can in fact occur in dense vegetation but also occur in hyper-arid deserts. Furthermore, we found hyaena densities were highest in these two habitats.

Geomorphological conditions explained differences in density estimates throughout the three sampled Mediterranean landscapes. Greatest densities were estimated at Mediterranean coastal shrublands. This area (Mt. Carmel) is famous for its abundant caves in comparison to inland Mediterranean habitat and highlands Mediterranean habitat. Coastal Mediterranean lithological and topographic characteristics contribute to cave formation mainly by karst collapse between limestone and dolomite rock mainly due to climate conditions near the coast (Barnes & Worden, 1998; Weinstein-Evron et al., 2012), and we believe that optimal conditions for cave formation can be a proxy for den formation as well. Following our logic, such conditions would be preferred by hyaenas due to den availability, therefore we assumed that greater densities would be documented at coastal Mediterranean habitats and our results agree. Den availability was previously reported to significantly influence hyaena densities in India (Akay et al., 2011; Alam, Khan, Kushawa, Agrawal, Pathak, & Kumar, 2014; Singh et al., 2010).

Low densities estimated at northern steppe can be explained too by geomorphological characteristics. This area lays strictly on extremely hard basalt bedrock, making den availability least probable in comparison to all other sampled habitats. In arid steppe sites, a habitat thought to be preferred by hyaena (Abisaid & Dloniak, 2015; Wagner, 2006), we documented low densities despite suitable geomorphological conditions.
Although we cannot state the exact nature for this estimation drop, a reasonable cause might be human development, which underwent massive land modifications, mainly to agriculture (47% of the region), leaving smaller and isolated natural patches throughout the landscape (Rotem et al., 2013). Due to their relatively large home-range (40–100 km² on average) (Tichon et al., 2016), it is possible that the remaining small and isolated patches of suitable natural habitats in this region cannot support larger hyaena populations (Shamoon, Cain, Shanas, Bar-Massada, Malihi, & Shapira, 2018).

Surprisingly, hyaena population densities in hyper-arid and arid highland deserts were similar to coastal and highland Mediterranean shrubland habitats. We expected to find low densities in oligotrophic desert habitats due to scarce resource availability (i.e. water availability and opportunistic food resources) (Abisaid & Dloniak, 2015; Wagner, 2006). While we advocate that den availability is a major limiting factor of hyaena densities, resource availability at desert areas must also be considered (Alam et al., 2015; Qarqaz, Abu Baker, & Amr, 2004; Wagner et al., 2008). A possible and likely explanation to relatively high densities in these environments is hyaena habituation to man-made resources. Hyaena use of open landfills was reported decades ago and the study highlighted the fact that hyaena numbers are high around landfills (Macdonald, 1978). Poor sanitation and access to landfills provide additional resources in arid habitats, thus increasing habitat carrying capacity (Bino et al., 2010; Shapira, Sultan, & Shanas, 2008).

We compared our estimates to six prior studies conducted in four regions within our study area and in bordering countries. Three studies used indirect signs as means to estimate densities (arid highlands: Van Aarde et al., 1998; northern inland Mediterranean shrubland: Abi-Said & Abi-Said, 2007, Reichmann, 2005), and three studies used camera traps as a way to collect data like the current study (Arid highlands: Tichon et al., 2016; arid steppe: Shamoon et al., 2018; coastal Mediterranean shrubland: Rosenberg et al., 2016) (Table 3). Our estimates did not agree with studies that used indirect observations (track and scat transects) to detect hyaena presence, but yielded higher estimation in arid deserts (compared to Van Aarde et al., 1998), and lower estimation in northern steppe and shrubland (compared to Reichmann, 2005 and Abi-Said and Abi-Said, 2007).

It should be noted the studies we compare our results to were carried out over a decade ago, and it quite possible that there was also a decrease in population size in these habitats; nevertheless, the differences between indirect signs and camera traps stands out. Making previous estimates that used indirect signs with the previous notion of solitariness less reliable in comparison to camera traps.

We further compared our results to other studies from the region that used camera traps. We found that our coastal Mediterranean shrubland estimates were extremely close to data from another study in the coastal shrubland (Table 3). Our estimates from the semi-arid steppe are slightly higher than estimates from semi-arid regions in the Shikma region of Israel, which is geographically adjacent to our semi-arid steppe sites with similar human development but with higher annual precipitation and water availability (Shamoon et al., 2018), making it probable to have a higher density. Last, we compared our results to a study carried out in arid desert highlands using a closed census estimation (Table 3). Our model estimate yielded a higher estimate. A likely reason for these differences is poor sanitation in proximity to human development. Tichon et al. (2016) sampled in extreme remote areas, while this study concentrated efforts closer to human development, therefore higher estimates in our sampled areas are most likely to occur.

We present a systematic and unified effort to assess distribution and population densities of the Striped Hyaena. Our findings contradict previous conceptions on Striped
Hyaena, such preferred use of open habitat or low density shrub habitats in arid to semi-arid environments and avoidance of true deserts (Abisaid & Dloniak, 2015). We found that hyaenans can thrive in dense vegetation when geomorphological conditions allow it, and the same in hyper-arid deserts when resources are available.

Supplementary Material
Supplementary Table S1 is available via the “Supplementary” tab on the article’s online page (http://dx.doi.org/10.1080/09397140.2019.1596589).

Disclosure statement
No potential conflict of interest was reported by the authors.

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References
Abi-Said, M., & Amr, Z. S. (2012). Camera trapping in assessing diversity of mammals in Jabal Moussa Biosphere Reserve, Lebanon. Vertebrate Zoology, 62, 145–152.
Abi-Said, M. R., & Abi-Said, D. M. (2007). Distribution of the Striped Hyena (Hyaena hyaena syriaca Matius, 1882) (Carnivora: Hyaenidae) in urban and rural areas of Lebanon. Zoology in the Middle East, 42, 3–14.
Abisaid, M., & Dloniak, S. M. D. (2015). Hyaena hyaena. The IUCN Red List of Threatened Species, 2015. https://www.iucnredlist.org/species/10274/45195080 (downloaded on 12.03.2019).
Akay, A. E., Inac, S., & Yildirim, I. C. (2011). Monitoring the local distribution of striped hyenas (Hyaena hyaena L.) in the Eastern Mediterranean Region of Turkey (Hatay) by using GIS and remote sensing technologies. Environmental Monitoring and Assessment, 181, 445–455.
Alam, M., Khan, J., Kushawa, S., Agrawal, R., Pathak, B., & Kumar, S. (2014). Assessment of suitable habitat of near threatened striped hyena (Hyaena hyaena Linnaeus, 1758) using Remote Sensing and Geographic Information System. Asian Journal of Geoinformatics, 14, 1–10.
Alam, M. S., Khan, J. A., & Pathak, B. J. (2015). Striped hyena (Hyaena hyaena) status and factors affecting its distribution in the giri national park and sanctuary, India. Folia Zoologica, 64, 32–39.
Arkin, Y., Ichoku, C., & Karnieli, A. (1999). Fault traces in the arid arava valley floor, israel, revealed by RADARSAT surface roughness classification. Canadian Journal of Remote Sensing, 25, 302–310.
Avni, Y., Porat, N., Plakht, J., & Avni, G. (2006). Geomorphic changes leading to natural desertification versus anthropogenic land conservation in an arid environment, the Negev Highlands, Israel. Geomorphology, 82, 177–200.
Ayal, Y., & Merkl, O. (1994). Spatial and temporal distribution of tenebrionid species (Coleoptera) in the Negev Highlands, Israel. Journal of Arid Environments, 27, 347–361.
Barnes, S., & Worden, R. H. (1998). Understanding groundwater sources and movement using water chemistry and tracers in a low matrix permeability terrain: the Cretaceous (Chalk) Ulster White Limestone Formation, Northern Ireland. Applied Geochemistry, 13, 143–153.
Bino, G., Dolev, A., Yosha, D., Guter, A., King, R., Saltz, D., & Kark, S. (2010). Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. Journal of Applied Ecology, 47, 1262–1271.
Danin, A. (1986). Flora and vegetation of Sinai. *Proceedings of the Royal Society of Edinburgh, 89*, 159–168.

Fiske, I. J., & Chandler, R. B. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software, 43*, 1–23.

Heydari, S. (2007). The impact of geology and geomorphology on cave and rockshelter archaeological site formation, preservation, and distribution in the Zagros mountains of Iran. *Geoarchaeology, 22*, 653–669.

Joseph, L. N., Elkin, C., Martin, T. G., & Possingham, H. P. (2009). Modeling abundance using N-mixture models: The importance of considering ecological mechanisms. *Ecological Applications, 19*, 631–642.

Kasparek, M., Kasparek, A., Gözcelioğlu, B., Çolak, E., & Yiğit, N. (2004). On the status and distribution of the Striped Hyaena, *Hyaena hyaena*, in Turkey. *Zoology in the Middle East, 33*, 93–108.

Kidron, G. J., Yair, A., & Danin, A. (2006). Dew variability within a small arid drainage basin in the Negev Highlands, Israel. *Quarterly Journal of the Royal Meteorological Society, 126*(562), 63–80.

Krishnaswamy, J., Bawa, K. S., Ganeshiah, K. N., & Kiran, M. C. (2009). Quantifying and mapping biodiversity and ecosystem services: Utility of a multi-season NDVI based Mahalanobis distance surrogate. *Remote Sensing of Environment, 113*, 857–867.

Macdonald, D. W. (1978). Observations on the behaviour and ecology of the Striped Hyaena, *Hyaena hyaena*, in Israel. *Israel Journal of Zoology, 27*, 189–198.

Neumann, F., Schötz, C., Litt, T., Hense, A., & Stein, M. (2007). Holocene vegetation and climate history of the northern Golan heights (Near East). *Vegetation History and Archaeobotany, 16*, 329–346.

Oindo, B. O., & Skidmore, A. K. (2002). Interannual variability of NDVI and species richness in Kenya. *International Journal of Remote Sensing, 23*, 285–298.

Phillips, L. B., Hansen, A. J., & Flather, C. H. (2008). Evaluating the species energy relationship with the newest measures of ecosystem energy: NDVI versus MODIS primary production. *Remote Sensing of Environment, 112*, 4381–4392.

Qarqaz, M. A., Abu Baker, M. A., & Amr, Z. S. (2004). Status and ecology of the Striped Hyaena, *Hyaena hyaena*, in Jordan. *Zoology in the Middle East, 33*, 87–92.

R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Rauch, H. W., & White, W. B. (1970). Lithologic controls on the development of solution porosity in carbonate aquifers. *Water Resources Research, 6*, 1175–1192.

Reichmann, A. (2005). *Population size and behavior of Striped Hyena in northern Israel* [in Hebrew]. Jerusalem: Israel’s Nature and Parks Authority (unpubl. report).

Rosenberg, B., Reichman, A., & Shamoon, H. (2016). *Striped hyena (Hayena hyaena) movement patterns near Haifa city, Mt. Carmel, Israel* [In Hebrew]. Jerusalem: Israel’s Nature and Parks Authority.

Rotem, G., Ziv, Y., Giladi, I., & Bouskila, A. (2013). Wheat fields as an ecological trap for reptiles in a semiarid agroecosystem. *Biological Conservation, 167*, 349–353.

Royle, J. A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics, 60*, 108–115.

Schmidt, H., & Gitelson, A. (2000). Temporal and spatial vegetation cover changes in Israeli transition zone: AVHRR-based assessment of rainfall impact. *International Journal of Remote Sensing, 21*, 997–1010.

Shamoon, H., Cain, S., Shanas, U., Bar-Massada, A., Malih, Y., & Shapira, I. (2018). Spatiotemporal activity patterns of mammals in an agro-ecological mosaic with seasonal recreation activities. *European Journal of Wildlife Research, 64*, 35, 1–10.

Shapira, I., Sultan, H., & Shanas, U. (2008). Agricultural farming alters predator-prey interactions in nearby natural habitats. *Animal Conservation, 11*, 1–8.

Singh, P., Gopalaswamy, A. M., & Karanth, K. U. (2010). Factors influencing densities of striped hyenas (*Hyaena hyaena*) in arid regions of India. *Journal of Mammalogy, 91*, 1152–1159.
Singh, R., Qureshi, Q., Sankar, K., Krausman, P. R., Goyal, S. P., & Nicholson, K. L. (2014). Population density of striped hyenas in relation to habitat in a semi-arid landscape, western India. *Acta Theriologica*, 59, 521–527.

Sneh, A., & Rosensaft, M. (2014). *Major exposed lithologic units of Israel and environs (1:500,000)*. Geological Survey of Israel. www.gsi.gov.il/?CategoryID=698&ArticleID=1768.

Somveille, M., Rodrigues, A. S. L., & Manica, A. (2018). Energy efficiency drives the global seasonal distribution of birds. *Nature Ecology & Evolution*, 2, 962–969.

Tichon, J., Rotem, G., & Ward, P. (2016). Estimating abundance of striped hyenas (*Hyaena hyaena*) in the Negev Desert of Israel using camera traps and closed capture-recapture models. *European Journal of Wildlife Research*, 63(5), 1–13.

Tourani, M., Moqanaki, E. M., & Kiabi, B. H. (2012). Vulnerability of Striped Hyenas, *Hyaena hyaena*, in a human-dominated landscape of central Iran. *Zoology in the Middle East*, 56, 133–136.

Van Aarde, R. J., Skinner, J. D., Knight, M. H., & Skinner, D. C. (1998). Range use by a Striped Hyena (*Hyaena hyaena*) in the Negev desert. *Journal of Zoology (London)*, 216, 575–577.

Wagner, A. P. (2006). *Behavioral ecology of the striped hyena* (*Hyaena hyaena*). Bozeman: Montana State University.

Wagner, A. P., Frank, L. G., & Creel, S. (2008). Spatial grouping in behaviourally solitary Striped Hyenas, *Hyaena hyaena*. *Animal Behaviour*, 75, 1131–1142.

Weinstein-Evron, M., Tsatskin, A., Weiner, S., Shahack-Gross, R., Frumkin, A., Yeshurun, R., & Zaidner, Y. (2012). A window into Early Middle Paleolithic human occupational layers: Misliya Cave, Mount Carmel, Israel. *PalaeoAnthropology*, 2012, 202–228.

Youngentob, K. N., Yoon, H.-J., Stein, J., Lindenmayer, D. B., & Held, A. A. (2015). Where the wild things are: using remotely sensed forest productivity to assess arboreal marsupial species richness and abundance. *Diversity and Distributions*, 21, 977–990.