

Article

Social interactions in striped hyena inferred from camera trap data: is it more social than previously thought?

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Abstract

Understanding the drivers promoting sociality over solitariness in animal species is imperative for predicting future population trends and informing conservation and management. In this study we investigate the social structure of a desert dwelling population of striped hyena *Hyaena hyaena*. This species is historically regarded as strictly solitary albeit being the least studied of the extant Hyaenids. Accumulating evidence regarding the frequency of social interactions suggests a revision of striped hyena social structure is required. We hypothesized that striped hyena has a social structure that is more complex than expected for a strictly solitary species. For that end, we deployed an array of camera-traps in a remote desert region in Israel, and compared observed frequencies of striped hyena co-occurrence against null models to test whether hyena co-occurred more than expected by chance. Seven adults were (re)captured by our camera-traps in 49 different instances over 83 tracking days. Of these, 6 exhibited shared space-use around a scarce, isolated perennial water source. Five of them, co-occurred with other hyena (in 3 instances) significantly more frequent than expected by chance (and that timing suggests reproduction is unlikely to be the driving factor). Our findings substantiate evidence of complex social structure in striped hyena, highlight the importance of a scarce resource in space-use and sociality, and provide a baseline for future research of striped hyena social structure. We suggest that similar methods be employed to evaluate social structure in other “solitary species” to better understand their social dynamics.

Key words: behavioral ecology, cluster in space, *Hyaena hyaena*, social interaction, striped hyena, social structure

The evolution of sociality with its fitness benefits and costs has occurred within a diversity of animal taxa. Understanding the drivers promoting sociality over solitariness and individual territoriality, and vice versa, is key to predicting future population trends as well as informing conservation and management. Accordingly, the search

for insights into the evolution of different social organizations and structures continues to motivate much behavioral ecology research (Macdonald 1983; Wrangham and Rubenstein 1986; Dammhahn and Kappeler 2009; Port et al. 2011; Dalerum 2012; Lühns et al. 2012; Perrin et al. 2012; Schradin et al. 2012; Schneider and

Kappeler 2014). However, key terms have been used inconsistently with respect to studies of sociality in animals, and here we follow Kappeler and van Schaik's (2002, but see also Kappeler 2019) call for standardization. Their framework describes a social system through 4 categories: social organization, social structure, mating system, and care system. The first 2 categories are most relevant to this study and consequently justify a brief explanation. "Social organization" describes the size and composition of a social unit (solitary, or, increased levels of gregariousness—e.g., pair-living and group living). "Social structure" describes the social interactions and communications among conspecifics (including social relationships/bonding and social behaviors).

Members of the order Carnivora exhibit a range of social organization from strictly solitary to highly gregarious (i.e., group-living; Gittleman 1989). Therefore, it is an informative taxon from which research can advance our understanding of drivers of sociality (Dalerum 2007; Schneider and Kappeler 2014). Several principles are regularly invoked as linked to increased sociality and clustering/grouping behaviors in carnivores due to selective pressures. The resource dispersion hypothesis, asserts that the distribution of resources is a factor that permits, facilitates, or constrains sociality (Macdonald 1983; Macdonald and Johnson 2015). Accordingly, a territory that has (for example) food-rich patches, and that can sustain more than 1 individual, can allow and may directly favor/drive the formation of a group, *sensu* gregariousness (Creel and Macdonald 1995; Gusset 2007; Valeix et al. 2012; Newsome et al. 2013), or the increased tolerance between conspecifics—leading to conspecific 'clustering in space' or 'shared space-use' (Dammhahn and Kappeler 2009). Other selective pressures that are invoked as promoting gregariousness and/or social behaviors in carnivores include: foraging, e.g., through cooperative hunting (Macdonald 1983; Wrangham and Rubenstein 1986); defense against predators, e.g., via increased communal vigilance, (Macdonald 1983; Wrangham and Rubenstein 1986); mating opportunities, e.g., through acquisition of mating opportunities (Wrangham and Rubenstein 1986); rearing young, e.g., via kin selection or alloparental care (Hamilton 1964; Watts and Holekamp 2007; Smith 2014); and reduction of the high costs of dispersal, e.g., via natal philopatry (Schneider and Kappeler 2014). In contrast, the costs of sociality can be high and include intraspecific competition on resources/mating opportunities (Sandell 1989), and increased transmission of parasite/diseases in a group (Kappeler et al. 2015) all of which may explain the high prevalence of solitary social organization in carnivores (Gittleman 1989).

Solitary species are defined as having very little contact with conspecifics (Gittleman 1989; Sandell 1989) which is manifested in spatiotemporal asynchrony in their activity and more specifically their movement throughout the habitat with conspecifics (Charles-Dominique 1978; Kappeler and van Schaik 2002; Dammhahn and Kappeler 2009). Accordingly, solitary species are not expected to exhibit social complexity or intentional social interactions—such as adaptive social strategies (Kappeler and van Schaik 2002; Dammhahn and Kappeler 2009). This description of solitary species can be considered as 'strictly solitary'. Nevertheless, being solitary does not imply a complete lack of social interaction but rather a more limited one (Kappeler and van Schaik 2002). A recent study by Elbroch et al. (2017) demonstrated that even species that exhibit solitary social organization (such as cougar *Puma concolor*) can, and sometimes do, participate in more complex social interactions (e.g., adaptive social strategies such as reciprocity) thus exhibiting increased complexity in their social structure. In general, 2 principles are invoked to explain social interactions and clustering in space

(that are not related to reproduction or territorial disputes) between solitary carnivore conspecifics. These are kinship (Hamilton 1964) and resource dispersion (Macdonald 1983; Wrangham and Rubenstein 1986).

Among solitary species, 'encounters' (co-occurrence; 2 individuals observed at the same time and place) and 'shared space-use' (2 individuals observed in the same location but not at the same time) can emerge, even without social preference (i.e., conspecific attraction), simply because individuals are independently attracted to resources. Therefore, for differentiating between 'random' encounters (*sensu* unintentional, asynchronized, independent of intraspecific attraction) and intended ones (i.e., synchronized or a result of intraspecific attraction), one could contrast between observed intraspecific co-occurrences and a null model that assumes a complete lack of synchronization/attraction among individuals.

Among the Carnivora, the Hyaenidae family, that includes 4 extant species (Holekamp and Kolowski 2009) is considered to be of particular interest as it contains the full range of social organization from strictly solitary to highly gregarious (Wagner 2006; Watts and Holekamp 2009). Hyaenids exhibit a gradient of gregariousness (Table 1) likely linked to dietary differences and variations in resource availability and distribution (Wagner 2006). The least studied Hyaenid is the striped hyena *Hyaena hyaena* (Mills and Hofer 1998; Watts and Holekamp 2007; Holekamp and Kolowski 2009; Wagner 2013), which is commonly considered to be solitary (Mills and Hofer 1998; Watts and Holekamp 2007; Wagner 2013) and even strictly solitary (e.g., "Striped hyenas lead a solitary existence and they are only rarely seen together", Kruuk 1976, p. 105). Due to its cryptic nature, there is a general lack of knowledge on the species' natural history and behavior. Specifically, data on its social organization and social structure that could inform population estimates and contribute to future conservation efforts are lacking (Abi Said and Dloniak 2015).

In this study, we evaluate the social structure of a population of striped hyena in Israel, and in line with accumulating evidence (e.g., Macdonald 1978; Rieger 1979; Heptner and Sludskij 1980; Bothma and Walker 1999; Wagner 2006; Wagner et al. 2008, see 'discussion' for further details), hypothesize that striped hyena will exhibit a more complex social structure and social interactions evidenced via higher levels of intraspecific encounters than expected by chance. We deem this behavior to be linked (at least partially) to resource dispersion/availability (in particular water, a scarce resource in our studied system). Moreover, we predict that individuals will exhibit greater space sharing at proximity to water sources. To test these predictions, we deployed an array of camera traps in the Negev Highlands (a remote desert region in Israel) and compared the observed co-occurrence data with a null model based on randomized data generated using settings based on those occurring in the study area. This study is the first to evaluate the spatiotemporal distribution of a striped hyena population in the Negev Highlands and assess its social structure.

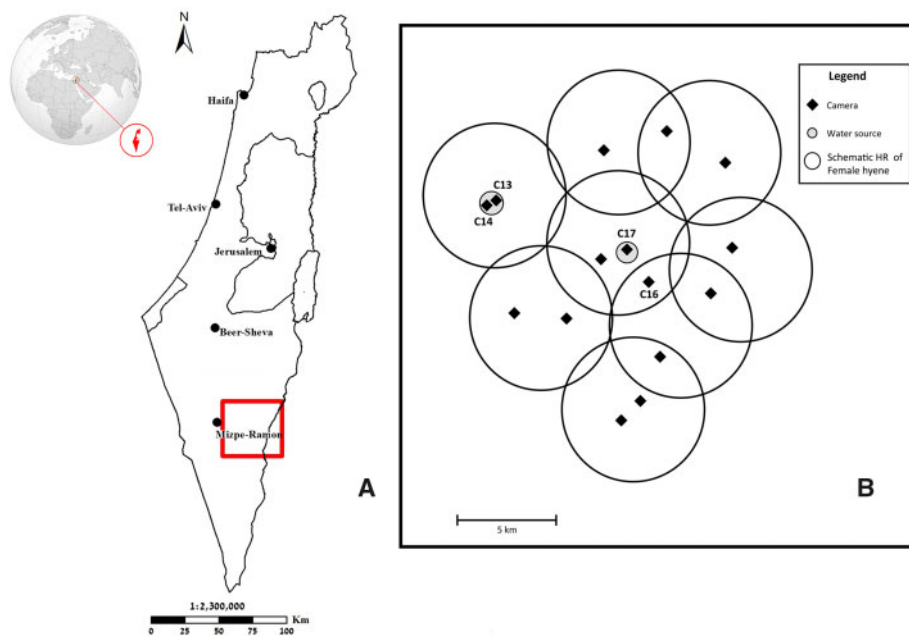
Materials and Methods

Study area

The study area spans *circa* 400 km² and covers a section of the Negev Highlands at the south of Israel (Figure 1A). This region is a hyper-arid (annual precipitation <80 mm) rocky mountainous desert that spans over 2,000 km² (Evenari et al. 1982). It is characterized by high plateaus that descend in steep slopes and cliffs (Hillel and Tadmor 1962). In the summer months (June–September), the

Table 1. Members of the Hyaenidae family in descending order according to their gregariousness (the order is provisional, as striped hyena social organization is not yet consensual)

Species	Social organization, structure (and gregariousness)	Number of adult individuals (per group)	Diet and foraging	Selective pressures favoring grouping	References
Spotted hyena (<i>Crocuta crocuta</i>)	Mixed-sex clans, fission–fusion societies	Up to 100	Carnivore: Hunt large ungulates, mostly (75%) solitary, otherwise cooperative hunting	Cooperative hunting, defend carcass versus competitors, intraspecific competition (defending clan territory), kin selection through den helpers	Holekamp et al. (2012), Smith et al. (2010), Wagner (2006), Watts and Holekamp (2007), and Watts and Holekamp (2009)
Brown hyena (<i>Hyaena brunnea</i>)	Mixed sex clans, female-bonded	Up to 14	Carnivore: Feed on small and dispersed food sources (e.g., small mammals, carrion), solitary forager	Intraspecific competition (defending clan territory), kin selection through den helpers	Watts and Holekamp (2007), Mills (1982, 1983), and Owens and Owens (1979)
Striped hyena (<i>Hyaena hyaena</i>)	Solitary or forming small groups/ clusters. Complex social structure?	Up to 7?	Omnivore: Feed on small and dispersed food sources (e.g., small mammals, carrion, vegetables), solitary forager	?	Wagner (2006), Bothma and Walker (1999), Heptner and Sludkij (1980), Macdonald (1978), Rieger (1979), Rieger (1981), Wagner et al. (2008)
Aardwolf (<i>Proteles cristatus</i>)	Socially monogamous pairs (exhibit sexually promiscuous behavior)	2	Insectivore: Solitary forager	Female increased foraging time in lactation necessitates paternal care	Watts and Holekamp (2007), Kotze et al. (2012), Marneweck et al. (2015), and Richardson and Coetzee (1988).

**Figure 1.** (A) The study area within the ‘Negev Highlands’ desert region at the south of Israel with an in-site showing the location of Israel. (B) A map presenting the array of 15 camera-traps (black diamonds) used during the study (labels refer to cameras with hyena captures). Cameras were deployed near key resources, including 2 perennial water sources (marked as small gray circles). The larger hollow circles (termed, HR zones) present schematic areas of the average home-range of a female striped hyena in Israel (about 60 km², Van Aarde et al. 1988). Cameras were spaced to maximize the chances that each (hypothetical, partially overlapping) HR-zone will be covered by at least 2 cameras.

driest and hottest time of the year temperatures can rise up to 44.8°C (mean annual temperature is ~19°C, Nativ et al. 1997). Most water sources in the region are ephemeral (following flash

floods in the rainy season) while perennial springs are scarce and dispersed making them a rare resource in a very warm and arid environment.

Study species

The striped hyena is listed in the IUCN Red List as 'near threatened' with a global population of <10,000 individuals, highly patchy distribution, and under continual decline (Abi Said and Dloniak 2015). An adult striped hyena measures total length (head to end of tail) 130–166 cm, height at shoulder 60–95 cm, and weight 25–55 kg (Rieger 1981), making it the largest and heaviest carnivore species in the Negev Highlands. The species lacks obvious sexual dimorphism, thus challenging the ability to determine sex remotely. It is an omnivorous scavenger feeding on small vertebrates (sometimes hunting them), invertebrates, larger carcasses, and anthropogenic-related resources including vegetables, fruits, and organic wastes (Wagner 2006). Across its distribution, parturition is reported to occur throughout the year (Rieger 1979); however, in Israel, the peak of parturition is reported to occur in the spring, i.e., March–April (Mills and Hofer 1998). The striped hyena is commonly considered to be a solitary carnivore (Kruuk 1976; Mills and Hofer 1998; Wagner 2013).

Camera traps

During the study, we used 15 Bushnell camera-traps (models 119678c, 119676c, 119477, 119537, 119437, and 119447) with passive infrared motion sensor (triggered by warmer-than-ambient objects that cross their detection range up to ~17 m away). We encased each camera in a camouflaged, protective box that was secured to rock faces. The cameras were used in 1 of 2 settings, either "camera only"—which takes 3 pictures per event after a trigger-time of 0.2 s, or 'hybrid'—which we set to take 2–3 pictures per event followed by a 10–15 s of video after ~2 s. In both settings, the camera had a 15 s 'rest' interval following a trigger event, before it could have been triggered again in a subsequent event.

Field methods and data collection

To maximize the cover by our array, the study area (*circa* 400 km²) was divided into 8 overlapping circular zones (Figure 1B) each representing approximately 60 km² which is equivalent to the smallest reported home-ranges (HR) of striped hyena in Israel—60 km² (Van Aarde et al. 1988) and 110 km² (The Society for the Protection of Nature in Israel [SPNI] n.d.) both for VHF-collared females in the Negev desert. The 15 cameras were spaced so that at least 2 cameras were placed in each hypothetical HR-zone to provide a full coverage of the study area. The locations of the HR-zones (Figure 1B) were designed to form an array that covered the entire study area (average distance between cameras = 2.53 km). The position of each camera within the HR zones was determined *in situ* following field surveys with local trackers and the cameras were often placed where signs of hyena and other wildlife (e.g., paw prints, scats) were abundant. Notably, 3 of the 15 camera traps (C13, C14, and C17) were placed on 2 perennial water sources. Camera C13 and C14 represent one spatial location (as they were placed approximately 200 m from each other on a perennial water source) and camera C17 was situated on another location also on a perennial water source. Cameras were deployed from the 22 July until the 12 October 2015 (83 consecutive days) summing to a total trapping effort of 1,245 trapping days. This data collection period corresponded with the Israeli summer (June–September).

Determining spatiotemporal distribution

We used the data from the camera trap array to test the hypothesis that striped hyena exhibit more frequent encounters than expected by chance. We take the capture of an individual hyena by a camera

trap to indicate its use of that area. Where more than 1 hyena was captured (non-simultaneously) by a camera trap, we take that to indicate overlap in space-use (i.e., 'shared space-use' or cluster in space). If these captures were within 24 h from each other we consider it as 'proximate shared space-use'. Instances of more than 1 individual captured in the same place at the same time are 'co-occurrence'. Furthermore, for hyena that were captured by more than 1 camera, the minimal area to be covered in between those cameras was taken as the minimal area of overlap between their HRs (i.e., the area that they share in common).

Contrasting observation with null model randomizations

To determine if observed frequencies of shared space-use and co-occurrences are more than expected by chance, we compared our observations with expectation derived from a null model assuming fully independent space-use among individuals (see Spiegel et al. [2016, 2018] for a more thorough discussion of this approach). Briefly, by using data permutations, we generated a distribution of expected frequencies under this null model. Constraining the permutations to the structure of the data allows us to account for differential use of the cameras (i.e., explicitly accounting for the fact that some cameras are located near resources that attract individuals independently of each other). We created 10,000 realizations of the null model, each including the same number of total hyena observations ($N = 49$), and the same camera specific frequencies (e.g., 42 instances of observations in camera C17) and sampling nights. For determining the timing of these permuted observations in each realization we first calculate the number of instances that 2 or more individuals will be captured by the same camera during a 24 h period—allowing us to test 'intention' in proximate shared space-use. Then, we draw observation times from the empirical distribution to determine for each dyad if they also co-occurred. Significance level of the camera-trap data (i.e., how likely was this data to happen by chance) is determined as the number of iterations in the simulated null model with encounter frequencies similar or higher than the observed (i.e., how many iterations it took to produce output equivalent to the observed data).

Results

Hyena observation in the camera array

Throughout the 83 trapping days of this study we captured 19,445 photographs and 1,831 videos of wildlife, including: Nubian ibex *Capra nubiana*, Asiatic wild ass *Equus hemionus*, Arabian wolf *Canis lupus arabs*, Arabian red fox *Vulpes vulpes arabica*, Blanford's fox *Vulpes cana*, caracal *Caracal caracal*, and African wildcat *Felis lybica* (not an exhaustive list). There was no co-occurrence of striped hyena with any of these species. From this footage, 357 pictures and 5 videos (1.7% of the total footage) were of striped hyena. Eight individual hyena (7 adults and 1 juvenile, in the first year of its life, based upon size) were captured (named H1–H8) in 51 distinct encounters (49 of which included adult hyena). Hyena H8 was identified as a juvenile associated with H2 (a female—identified by her maternal nipples), while the rest were adults of unknown sex. As H8 was considered to be a dependent juvenile (always associated with adult female H2) we do not consider H8 in analysis and interpretation of co-occurrence or proximate shared space-use. The estimated abundance of adult hyena in the study area was $\hat{N} = 7$ (for further details see Tichon et al. 2017). Results of

camera trap footage with adults are summarized in Table 2. Notably, all individuals were captured by camera C17, positioned on a perennial water source and 3 additional cameras were responsible for the remaining captures (C13, C14, and C16, see Figures 1 and 2).

Joint observations and HR overlap

All co-occurrences that were documented throughout the study are summarized in Table 3. Camera C16 (positioned on a col about 1 km south-east of camera C17—see Figure 2, and operational for only 37 days) captured 1 occasion in which 2 individuals were co-occurring (H3 with H4, see Figure 3A). Camera C17 (situated on a perennial water source) captured 2 occasions in which 2 individuals co-occurred (H3 with H5, and H1 with H7, see Figure 3B, C, respectively). Over the duration of the study, 7 adult hyena (H1–H7) and 1 juvenile (H8) were captured by camera C17. Six of these adults were captured on more than 1 occasion while individual H6 was only captured once (thus, this location is not necessarily a part of its permanent HR). Therefore, the location of camera C17 is considered a point of overlap between the HRs of 6 adult hyena (after excluding H6 and H8). Accordingly, these hyena are considered to share, at the minimum level, that point in common within their

Table 2. Adult striped hyena observations at the Negev highlands by camera and individual ID during the study period (F=female)

Hyena ID	Observations by camera				Total observations
	C13	C14	C16	C17	
H1	1	2	1	8	12
H2 (F)	0	0	0	18	18
H3	0	1	1	2	4
H4	0	0	1	2	3
H5	0	0	0	6	6
H6	0	0	0	1	1
H7	0	0	0	5	5
Total	1	3	3	42	49

HRs. H4 was also captured in the location of camera C16. H1 and H3 were captured at all 3 camera locations that captured hyena, i.e., also by camera C13 and C14 (both located on a perennial water source approximately 10 km west of camera C17, and about 200 m from each other) and with one of these hyena involved at each of the 3 co-occurrences (Figure 3). In accordance, we inferred a minimum overlap between the HRs of these hyena (H1, H3, and H4) that exceed the location of camera C17 (Figure 2).

Shared space-use and social interactions

Our results demonstrate that shared space-use occurred at specific locations (hyena encounters occurred at 4 out of 15 camera traps). Mostly, these locations were in the proximity of resources (i.e., perennial water sources). In 7 instances, different individuals were observed at the same camera within a 24 h period. These instances include both co-occurrences and 'proximate shared space-use' (Table 3). This frequency of proximate shared space-use is not significantly different ($P = 0.72$) to null expectations accounting for the sampling effort (camera specific activity duration), and camera differential capture success (Figure 4A). Nevertheless, the observed frequency of co-occurrence ($N = 3$) is significantly higher than null expectation ($P = 0.0023$), in which only 23 instances out of 10,000 modeled yielded 3 or more instances of co-occurrence. This result demonstrates that hyenas show conspecific attraction beyond shared space-use, are clustering in space and time, and suggests that they exhibit a more complex social structure than the term 'strictly solitary' implies.

Discussion

In this study, we tested the hypothesis that striped hyena, despite historically being considered strictly solitary, exhibit social interactions and spatiotemporal overlap suggesting a more complex social structure. With our camera-traps, we documented 7 adult hyena, 6 of which exhibited a shared space-use of varying degrees (from sharing 1 spatial location by all of them, to sharing 3 distant locations by 2). In addition, we documented 3 co-occurrences of adult hyena (2 of

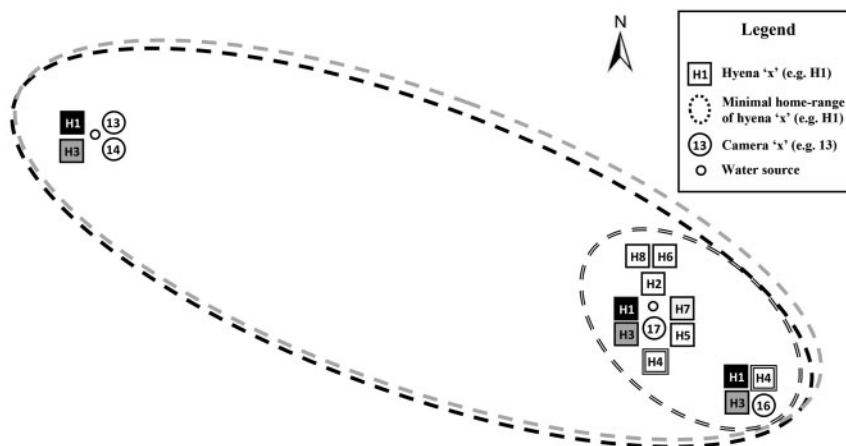


Figure 2. A schematic map (not to scale) depicting the locations where the 8 hyena were (re)captured. Each hyena is marked by its codename (e.g., H1) and, if observed in more than 1 location, also by a distinct color. The dashed ovals represent the (schematic) minimal home-range that is expected to be covered by the hyena that were (re)captured in more than 1 camera location (i.e., H1, H3, and H4). The color/pattern of the dashed line corresponds to the color/pattern of the associated hyena (i.e., H1-black, H3-gray, H4-double-line). All hyena were captured at the location of camera C17 (the one that is encircled by all hyena) and it is thus considered to be a point of overlap where all home-ranges meet. H6 and H8 are not included in this consideration of overlap as H6 appeared only once and H8 is a juvenile.

Table 3. Hyena dyads' co-occurrences and proximate shared space use (indicated by the time difference between the occurrences of the different hyena)

Date	Camera	ID1	Time 1 (hh:mm:ss)	ID2	Time 2 (hh:mm:ss)	Time difference (hh:mm:ss)
24 July 2015	C16	H4	02:38:04	H3	02:38:04	Co-occurrence
23 July 2015	C17	H2	03:06:43	H3	22:52:42	Circa 20 h (19:45:59)
07 August 2015	C17	H6	01:01:00	H3/H5	21:26:30	Circa 20 h (20:25:30)
07 August 2015	C17	H5	21:26:30	H3	21:26:30	Co-occurrence
17 August 2015	C17	H2	21:35:20	H4	21:54:46	Circa 20 min (00:19:26)
18 August 2015	C17	H7	21:55:54	H1	21:55:54	Co-occurrence
27 September 2015	C17	H1	03:43:37	H2	05:02:33	Circa 1.5 h (01:18:56)

**Figure 3.** These pictures show examples from the 3 instances in which dyads of hyena were captured simultaneously by a camera (i.e., co-occurring). (A) H3 and H4 captured by camera C16. (B) H3 and H5 captured by camera C17, and (C) H1 and H7 captured by camera C17.

which were located on a perennial water source and the third on a nearby col). We found that co-occurrences in our study took place more frequently than expected by chance (3 out of 49 that we encountered vs. 23 out of 10,000 in the null model simulation that accounted for structures and dependencies in the data). Our results demonstrate that the social interactions by the hyena were

'intentional' (i.e., meeting more than expected by chance if their use was independent of others) thus exhibiting conspecific attraction. Alternately, there could have been an external (perhaps environmental) cue, that we did not detect, that drives individual hyena to use the same area at the same time, and thus created an *apparent* conspecific attraction. Solitary species are expected to have very little contact with conspecifics and to exhibit asynchrony in general activity (especially in movement throughout the habitat with conspecifics). The striped hyena in our population deviated from this definition. Their shared space-use indicated overlap in HR on scarce water sources and their co-occurrences suggest intentional social interactions, evidencing a more complex social structure than expected from a 'strictly solitary'. This study presents the first documentation of such behavior in striped hyena that is tested against a null hypothesis of random encounters.

In all hyena co-occurrences, due to a lack of data on sex and relatedness, the relationship of association within dyads (e.g., breeding pair, siblings) could not be determined (excepting H2 and H8, inferred to be a mother and her offspring). However, due to their timing, these co-occurrences are unlikely to be motivated by reproduction. While striped hyena produce litters throughout the year in the wild (Rieger 1979), the peak of parturition in Israel is reported to be in the spring—i.e., March–May (Mills and Hofer 1998). With a gestation period of 90–92 days (Rieger 1979; Mills and Hofer 1998), mating in Israel is likely to occur December–February. All records of hyena co-occurrence in this study took place during July and August, thus outwith the likely mating period. Likewise, the shared space-use of the 6 adult hyena at the perennial water source of camera C17 also took place during July–September.

Supporting evidence of sociality in striped hyena

Despite historically being considered as a strictly solitary species (Kruuk 1976; Mills and Hofer 1998; Wagner 2013), accumulating evidence suggests that the striped hyena social structure is more complex. Heptner and Sludskij (1980) describe the occurrence of monogamous pairs and groups of up to 5–6 in Central Asia. Holekamp and Kolowski (2009) report on groups of up to 7 occurring in North Africa (i.e., Libya). In Kenya, striped hyena were frequently observed resting in pairs and on occasion in groups of up to 4 individuals (Wagner 2006; Wagner et al. 2008). These groups consisted mostly of unrelated or distantly related hyena (on occasion containing full siblings: brother–brother or brother–sister) and were always mixed sex with 1 female and up to 3 males (Wagner 2006; Wagner et al. 2008). Wagner (2006) reported 2 sub-adult female siblings in Kenya that were observed regularly at the den of their mother assisting with rearing new born cubs. Striped hyena cubs have also been reported to be attended by adult males (the father and sometimes more than 1 male) until independence in the African

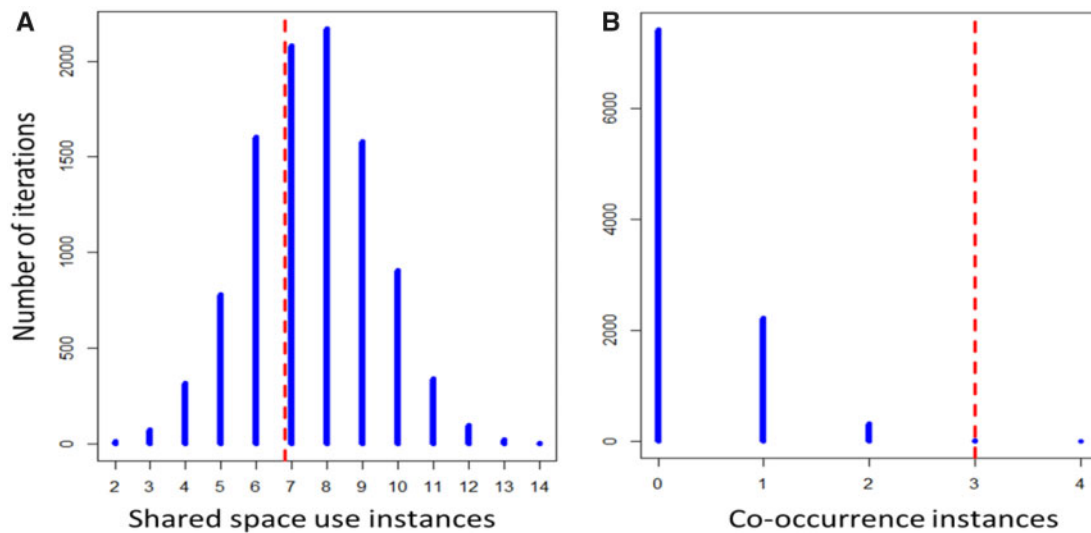


Figure 4. Shared space-use and social interactions in striped hyena. Results from a permutation test contrasting observed frequency (vertical dashed lines) of (A) proximate shared space-use (individuals captured at the same camera during a 24 h period) and (B) co-occurrence (individuals captured in the same camera at the same time) with expectations from null model assuming space use is independent among individuals and accounting for camera specific sampling effort and capture frequencies. These results (dashed lines) demonstrate that while hyena in the studied population readily share space, this rate is not different from expectations based on resource distribution. Nevertheless, this analysis reveals that hyena co-occurred significantly more than expected from shared space-use alone.

savannah (Bothma and Walker 1999). For Israel's striped hyena, Macdonald (1978) reported ≥ 2 striped hyena moving and eating together in more than half of his observations (9 out of 16, including 7 observations of 2 individuals, 1 observation of 3 individuals, and 1 observation of 4 individuals) all at a feeding site of the Israeli Nature and Parks Authority (INPA) in the Judean Desert, Israel. Groups of up to 4 individuals were seen moving along and feeding simultaneously on several occasions at other feeding sites of the INPA in the north of the Judean Desert, Israel (Erez Baruchi and Shachar Kfir—INPA Rangers, personal communication, November 2016). Lastly, a pair of subadult striped hyena was reported as arriving together to an INPA feeding site in the Negev Highlands, Israel (Skinner and Ilani 1979).

Altogether, the data presented in this study contribute further to accumulating evidence of a more complex social structure than 'strictly solitary' in striped hyena. Moreover, it presents the first account of hyena co-occurrences in Israel on a resource that is not food, thus underscoring the importance that scarce perennial water sources might have in driving social interactions and clustering in space in arid environments. Furthermore, contrary to the aforementioned examples, we were also able to show that even after accounting for the attraction to key resources the observed frequencies exceed those expected by independent space-use. These aspects contribute to our understanding of social structures and their driving forces in species that are otherwise considered to be strictly solitary.

Drivers and conditions explaining striped hyena space clustering

Striped hyena are reported to remain in the vicinity (up to 10 km) of water sources (Rieger 1979, 1981), especially during the warmer period of the year (Heptner and Sludskij 1980) which in Israel is June until September. Such behavior indicates dependence on water sources. Considering this, the formation of a cluster of adult hyena exhibiting shared space-use around the location of camera C17 is

likely linked to its proximity to a scarce and isolated perennial water source. Macdonald et al. (1999) describe a population of red fox dwelling in a Saudi Arabian desert that exhibit a loose-sense of territoriality unlike red fox populations elsewhere. Their proposed explanation is that existing harsh environment and dispersed scarce resources (in this case, food-rich dumps and shadow) require forming large territories that are difficult to defend thus favoring the formation of a shared space-use cluster. The cluster of striped hyena that we describe persists in similar conditions where a scarce resource (water) could have led to increased tolerance and consequently a lack of strict territoriality. Possibly, such spatial overlap intensifies during the dry summer months when all ephemeral water sources are completely dry, but this is impossible to test with our dataset. The formation of such a shared space-use in terms of the scarcity and dispersion of water as a resource is consistent with the resource dispersion rationale (*sensu* Macdonald and Johnson 2015). Resource dispersion provides an explanation for a driving (or at least a facilitating) mechanism by which the formation of such clustering in space could be favored.

The hyena in our study could potentially socialize during the day at resting points similar to a population described from Kenya (Wagner 2006; Wagner et al. 2008). The hyena female (H2) may have had assistance at the den in rearing the juvenile (H8) from the father (as for Heptner and Sludskij 1980; Bothma and Walker 1999), other males from the cluster (Bothma and Walker 1999), and/or subadult siblings (Wagner 2006). Lastly, the described space-sharing cluster could be a philopatry-based family group (as described in Heptner and Sludskij 1980; Bothma and Walker 1999), contain monogamous pairs (as reported by Heptner and Sludskij 1980), or be polyandrous (Wagner et al. 2008) or polygynous in mating system.

We suggest that future research on striped hyena should focus on several parallel areas. Firstly, direct behavioral observations are required, e.g., using more camera traps over longer periods (while taking video footage) to evaluate the nature of the social interactions

(upon co-occurrence) and thereby to understand the extent of the complexity of their social structure. Such data would enable social network analyses to be conducted. Secondly, future research should aim at higher resolution spatiotemporal data (e.g., from GPS collars) and data on age-sex and genetics (DNA, e.g., from feces/blood).

Conservation implications

Defining a species as solitary can ultimately bear consequences for its protection. For example, abundance estimates of the IUCN Red List often assume a linear relationship between species' abundance and area of occupancy (Akçakaya et al. 2006). Accordingly, a region that was previously assumed to host a particular number of solitary individuals will accommodate more if the species exhibits clustering behavior and shared space-use. Moreover, establishing the complexity of the social structure of striped hyena, as well as its clustering in space, has important implications for conservation efforts of this elusive and under-studied species. On the one hand, current abundance estimates in the IUCN Red List species account are based on the assumption that the striped hyena is a strictly solitary species that lives at low densities (Mills and Hofer 1998; Abi Said and Dloniak 2015). Consequently, our findings that the striped hyena in our study exhibited social interactions and shared space-use suggests that current estimates of abundance/density of striped hyena may be underestimated. On the other hand, should cooperative care (if occurring) promote the species' reproductive success, as for spotted and brown hyena (Table 1), decreasing population density and increasing fragmentation of populations may have serious implications for the future sustainability of wild striped hyena populations, e.g., via an 'Allee effect' (Allee et al. 1949; Courchamp et al. 1999).

In light of accumulating evidence, it is time to change the default assumption that the striped hyena is a strictly solitary species (Mills and Hofer 1998). The evidence from across its range and in this study suggests that under some conditions, and in accordance with resource dispersion rationale, striped hyena sometimes cluster in space (i.e., shared space-use) and exhibit social interactions that suggest a more complex social structure. The striped hyena, the least studied of the Hyenids, receives a much undeserved bad reputation and is persecuted across its range (Holekamp and Kolowski 2009; Wagner 2013). In part, this undeserved reputation is the result of past accounts of hyena that raided human graves (Leakey et al. 1999; Wagner 2013), caused damage to agriculture and livestock (Wagner 2013), and legends of them enchanting people and dragging them to a den where they eat them (e.g., in the Middle East, Qarqaz et al. 2004). Combined with a declining availability of food, the striped hyena has been extirpated in many areas and populations continue to decline (where known) across their range (Abi Said and Dloniak 2015). With a better understanding of striped hyena ecology and social structure we can address some of the threats that imperil its future and enhance the conservation of this fascinating species.

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Conflict of Interest Statement

The authors declare that they have no competing interests.

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