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Inter-dependent movements of Asiatic Cheetahs *Acinonyx jubatus venaticus* and a Persian Leopard *Panthera pardus saxicolor* in a desert environment in Iran (Mammalia: Felidae)

Farid Cheraghi[a,c], Mahmoud Reza Delavar[b,*], Farshad Amiraslani[a], Kazem Alavipanah[a], Eliezer Gurarie[c], Houman Jowkar[d], Luke Hunter[e], Stephane Ostrowski[e] and William F. Fagan[c]

[a]*Department of Remote Sensing and GIS, Faculty of Geography, University of Tehran, Tehran, Iran;* [b]*Center of Excellence in Geomatic Engineering in Disaster Management, School of Surveying and Geospatial Engineering, College of Engineering, University of Tehran, Tehran, Iran;* [c]*Department of Biology, University of Maryland, College Park, Maryland, USA;* [d]*Conservation of Asiatic Cheetah Program, Department of Environment, Tehran, Iran;* [e]*Wildlife Conservation Society, Bronx, New York, USA*

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We investigated the simultaneous and sympatric movements of a coalition of two Asiatic Cheetahs (*Acinonyx jubatus venaticus)* and a Persian Leopard (*Panthera pardus saxicolor),* two rare and highly mobile large felids in Bafq Protected Area, Iran. The animals were tracked with GPS collars for 4.5 to 9 months at a temporal resolution of eight hours. The cheetahs used lower elevations areas (average: 1600 m), and remained more distant to the surrounding highways of (average: 14.5 km) than the leopard (average: 1.8 km and 12.3 km, respectively). The leopard's home range (408 km^2) was almost entirely within the larger home ranges of the cheetah coalition (1,137 km^2). We found that the leopard approached more closely to either of the cheetahs in the rare occasions when they were separated, though whether that was the response of the cheetahs to the leopard or vice versa is unknown. This interaction eventually culminated in the leopard killing one of the cheetahs, the first documented proof of lethal competition between cheetah and leopard in Iran. The combined risks of larger home ranges beyond the protected areas with higher probability of encounters with humans, of highway crossing, and predation by Persian Leopards contribute to the particularly precarious situation of the Asiatic Cheetah.

Keywords: Spatial ecology; wildlife interaction; GIS; wildlife tracking

Introduction

Many large cats in the wild are globally imperilled, but few are as critically endangered as the Asiatic subspecies of the Cheetah (*Acinonyx jubatus venaticus)*, with a population of only 50–70 individuals in the wild, entirely constrained to central Iran (Durant et al., 2016; Farhadinia et al., 2017). One of the major challenges of Asiatic Cheetah conservation is the anticipated very large size of their home ranges – around 2100 km^2 (±SE 800 km^2) (Farhadinia et al., 2016) – necessary in their largely arid and low-productivity environment, but which are generally larger than most existing protected habitat reserves (Moqanaki & Cushman, 2017). Their movement behaviour and habitat use have previously been described by Cheraghi, Delavar, Amiraslani, Alavipanah, Gurarie, Fagan, 2018.

*Corresponding author. Email: mdelavar@ut.ac.ir

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The Persian Leopard (*Panthera pardus saxicolor)* is also considered endangered (IUCN, 2008), with an estimated population between 850 and 1300 mature individuals in the wild. The Persian Leopard ranges from the Caucasus region across northern Iraq and Iran to southern Turkmenistan and central Afghanistan. The majority of the population is found in Iran (estimated 550–850 individuals; Sanei et al., 2016), mainly in the northern parts of the country, but also in mountain areas of the central plateau where its geographic range overlaps with that of the Asiatic Cheetah. In Iran, Persian Leopards typically have larger home ranges than elsewhere in their global geographic ranges as shown in Tandoureh National Park in the north-east of Iran, with a home range area of 103.4 km^2 (±SE 51.8 km^2) (Farhadinia, Johnson, Macdonald, & Hunter, 2018) using auto-correlated kernel method compared to leopards in Thailand, where Simcharoen, Barlow, Simcharoen, and Smith (2008) found a home range area of 30.54 km^2 (± SE 9 km^2) using a fixed kernel method. There is no information on the Persian Leopard home range and movement behaviour in the central arid environment of Iran.

Along with some geographical overlap, leopards and cheetahs in central Iran display niche overlap, with concomitant anthropogenic pressures. Both species preferentially feed on ungulates, particularly Chinkara (*Gazella bennettii*), Bezoar Goat (*Capra aegagrus)* and Wild Sheep (*Ovis orientalis*) (Farhadinia & Hemami, 2010; Sharbafi, Farhadinia, Rezaie, & Braczkowski, 2016*)*. Finally, both felids are seriously threatened in Iran due to anthropogenic habitat modification, vehicle strikes on roads, retaliatory persecution by livestock owners and poaching by humans (Farhadinia et al., 2017; Sanei et al., 2016). Like their African relatives, Asiatic Cheetahs may also be subject to predation and kleptoparasitism by other predator species, although this hypothesis still requires documentation. Given the extreme rarity of these species, telemetry data are scarce, and data on their interactions are even sparser.

Spatial interactions among wild animals have been the subject of extensive research, with previous work divided into two main categories based upon whether space use was viewed from a static or dynamic perspective. The static methods analyse spatial occurrence data without taking the time of observation into account (e.g., the animals' home-range overlap percent; Millspaugh, Gitzen, Kernohan, Larson, & Clay, 2004). In contrast, dynamic methods explicitly account for the timing of occurrences and are typically tailored for animal movement data. Dynamic approaches further divide into two categories: distance-based and path-based (Long, Nelson, Webb, & Gee, 2014). The distance-based methods follow a spatial point pattern paradigm. This means that they calculate the Euclidean distance between two animals at simultaneous observations and introduce this distance as a measure of social interaction, subsequently comparing the observed versus expected distributions of distances (Long et al., 2014). In contrast, path-based methods consider animal movement tracks as vectors of movement, and quantify the similarity or cohesiveness of movements among individuals. Importantly, the path-based methods do not explicitly account for absolute spatial position (Long et al., 2014). At the extreme, these methods allow movement paths to be cohesive even when separated by great distances; for example, the track of two distant animals moving at the same speed and to the same direction are considered to be cohesive (Calabrese et al., 2018). We combine both the static and dynamic perspectives to better understand the interactions between the animals (Cheraghi, Delavar, Amiraslani, & Alavipanah, 2018).

In this study, we analyse a unique simultaneous and sympatric movement dataset from a coalition of two Asiatic Cheetahs and a Persian Leopard monitored in the arid central plateau of Iran. We hypothesized that their movement behaviour (e.g. moving or encamped) and habitat preferences are different, and their movements are not independent from one another. We were interested, first, in comparing and contrasting these species' movement behaviours and habitat selection and, second, in attempting to identify whether proximity between them had any influence on their movement behaviour. To this end, we made two assumptions: The path between consecutive GPS data points is traversed linearly; the movement behaviour at a current state is auto-correlated with the previous state. Eventually, we attempted a hybrid approach, combining both the static and dynamic methods, to analyse interaction on their movement..

Material and Methods

Study area. The 885 km^2 large Bafq Protected Area (31°37'N, 55°38'E), 42.5 km east-west 50.3 km north-south) is characterised by desert and xeric shrubland habitat with scant rainfall (average annual rainfall over 22 years 62 mm), high temperature and degraded landscape (Amiraslani & Dragovich, 2011; Freitag, 1986). The Conservation of the Asiatic Cheetah Project (CACP) identified Bafq as one of the ten key protected areas for the conservation of Asiatic Cheetah. In addition to cheetahs and leopards, Bafq Protected Area hosts Bezoar Goat, Wild Sheep, Chinkara (*Gazella bennettii*) and Cape Hare (*Lepus capensis*). Other carnivores present include Striped Hyaena (*Hyaena hyaena*), Grey Wolf (*Canis lupus*), Caracal (*Caracal caracal*), Eurasian Golden Jackal (*Canuis aureus*), Red Fox (*Vulpes vulpes)* and Blanford's Fox (*V. cana*). Bafq Protected Area is roughly delineated to the north by two highways, and contains 28 water sources in the form of small artificial and natural pools and springs, 7 small villages and settlements, and a network of dirt paths created by trampling by humans and livestock (Figure 1A).

Environmental data. We collected data on climate including temperature, humidity, pressure, wind speed and direction from the nearest synoptic weather station within 10 km of Bafq Protected Area. We used the digital elevation model from the Shuttle Radar Topography Mission (SRTM), and extracted elevation and slope at all animal locations. It is assumed that elevation and slope are proxies for the occurrence of the cats' prey, because the primary prey at the site—Wild Sheep and Bezoar Goat—mainly inhabit foothills and mountain slopes (Farhadinia, Moqanaki, & Hosseini-Zavarei, 2014; Hunter et al., 2007). Elevation, slope, distance to nearest water, distance to nearest human pathway, distance to nearest highway, distance to nearest village and temperature were the environmental covariates used in our analyses of cheetah and leopard movement and habitat use (see below; Supplementary Data 1).

Movement data: One Persian Leopard (PL, age 7–10 years) and two male cheetahs (C1 and C2, age 3–5 years) were captured in the Bafq Protected Area using foot snares after 512 trap nights in February, 2007, under permits from the Iran Department of Environment. The animals were instrumented with GPS collars (Vectronics, Germany) and the collars were programmed to transmit locations every 8 hours (at 00:00, 08:00 and 16:00). The data were retrieved periodically by uploading to a hand-held receiver via UHF radio link. The two cheetahs were members of a male sibling coalition, a common social grouping among non-reproductive cheetahs (Kingdon, 2015). Based on the similarity of their movement statistics and proximity (see results), we used C1, which had somewhat more observations, as a proxy for both cheetahs' movements in several analyses.

Analysis methods. To analyse interactions using a static approach, we computed the animals' home range using the 100% and 95% minimum convex polygon (MCP; Mohr, 1947) of the tracks after visually excluding outlying points. We then computed the spatial intersection of the two MCPs and the area of all resulting polygons to obtain an estimate of the animals' home range and overlapping area. We chose MCP for its simplicity and general conservatism, as the data were short in overall duration to effectively estimate, for example, a kernel density estimator (Fleming, Fagan, Mueller, Olson, Leimgruber, & Calabrese, 2015). To characterise the movement behaviour, we modelled the movements of both cats as a multi-state correlated random walk with two behavioural states and probabilities of transitions between the states governed by a Hidden Markov Model (HMM, Michelot, Langrock, & Patterson, 2016). We defined the two states as a *moving* behaviour, characterised by more linear, longer-distance displacements, and an *encamped*

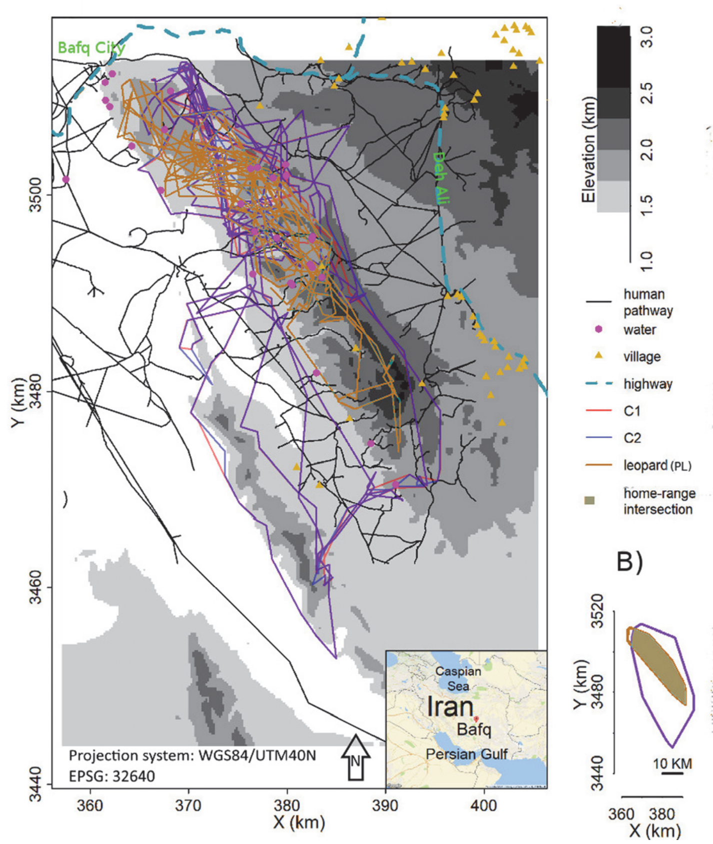

Figure 1. A) Map of study area superimposed by human pathway, highways, villages, water sources and animal tracks. The tracks of the cheetah coalition are almost identical, which is evident from the purple colour produced by overlapping transparent red and blue. B) Home range comparison of the cheetah 1 (C1) and the Persian Leopard (PL) during the same temporal interval. The tracks are clipped to intersecting temporal range and the distances are computed at simultaneous fixes occurring at 00:00, 08:00 and 16:00.

behaviour, characterised by greatly reduced or zero movement during an observation interval (Cheraghi, Delavar, Amiraslani, & Alavipanah, 2017). We compared the estimated behavioural states of C1 and PL to test for cohesiveness – similarity of movement behaviour at simultaneous locations – in their movement behaviours using Chi^2 tests (Hope, 1968). We analysed the interaction dynamically using a distance-based approach, and regressed the C1-C2 distance against C1-PL distance to assess whether the large-scale separations of the cheetah coalition was related to proximity of PL.

To explore the habitat preferences of animals, we estimated a Resource Selection Function (RSF; Boyce & McDonald, 1999). To obtain an availability null set (i.e. unused locations, or "pseudo-absences"), we randomly sampled within the MCP. We then fitted a logistic regression with the presences and pseudo-absences of the animal as the response variable, variously including linear, second order, square root and log of the environmental terms as covariates. We employed best subset selection (scored by Akaike Information Criteria, AIC) to identify significant covariates (Burnham, Anderson, & Huyvaert, 2011). We used variance inflation factors (VIF) to check for the absence of multi-collinearity in our regression models (Fox & Monette, 1992).

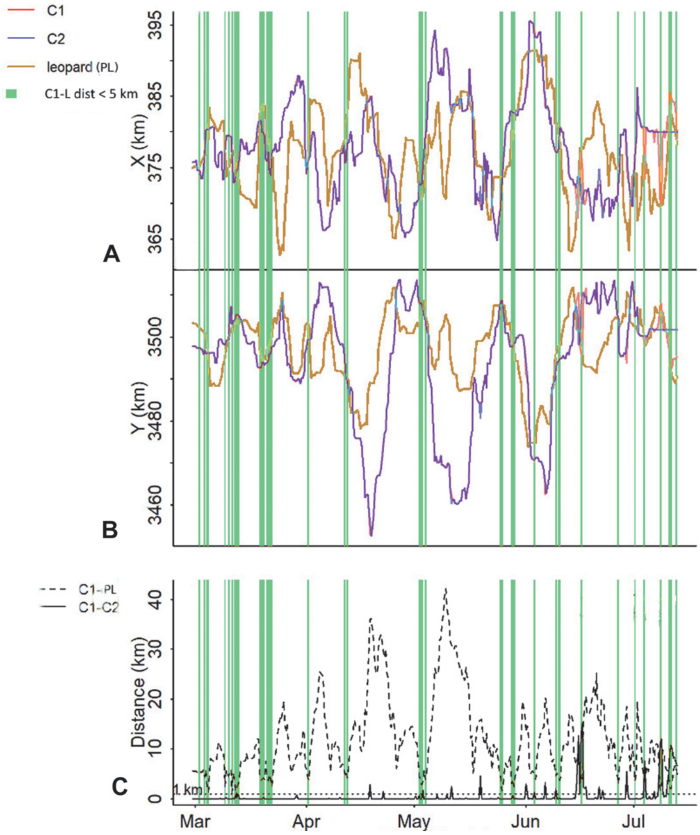

Figure 2. A-B) X and Y coordinate time series profile of the movement data. C) Time series of C1-PL and C1-C2 distances. In all panels, the tracks are clipped to intersecting temporal range, and the distances are computed at simultaneous fixes occurring at 00:00, 08:00 and 16:00.

Results

The two cheetahs, C1 and C2, and the Persian Leopard (PL) were collared on 27, 26 and 29 of February 2007, respectively, and their collars transmitted for 130, 137 and 282 days, again respectively. There were relatively few missing points for C1 and C2 (4.5% and 7%, respectively) and the gaps were mainly one-step (16 h interval) with very few two-step gaps (24 h interval). For PL, 34% of the observations were missing, with 153 one-step and 47 two-step gaps; the numerous gaps could have been due to PL residing and ambushing under the bushes and rocks that hindered the visibility of GPS satellites as has been described by Moen, Pastor, Cohen, and Schwartz (1996) for moose under a conifer or deciduous canopy. In total, C1, C2 and PL tracks consisted of 443, 410 and 846 locations, respectively, after the linear interpolation of the missing points; 405 of these locations were simultaneous. C2's collar seemed to have been lost and it was found still closed with no cheetah around on July 13, 2007 and four days later PL killed C1. We concluded this based on C1's GPS track ceasing movement within 8 hours after a minimum C1-PL distance of 0.49 km (Supplementary Data 3; frames 408-415) and post-mortem findings. C1's carcass was found too late for a thorough necropsy to be done but the presence of distinct lateral and dorso-lateral perforations of the skull and

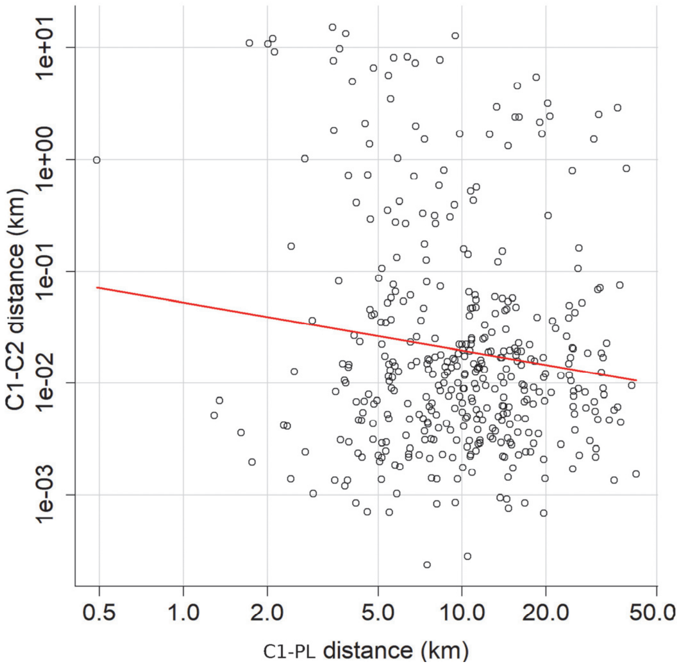

Figure 3. Relationship between the distance between the two cheetahs (C1-C2 distance) and the distance between cheetah C1 and the leopard (C1-PL distance) (N=405). Red = regression line. Note the double log plot: the graph is drawn with the axes on a log scale and the regression model is fitted to the log of C1-PL and C1-C2 distances. The tracks are clipped to the intersecting temporal range, and the distances are computed at simultaneous fixes occurring at 00:00, 08:00 and 16:00.

neck combined to dry blood, and to what could have been dry saliva on the skin of the neck, were very supportive of a lethal leopard bite (Figure 4Figure 1).

Before the death of C1, the movements of the two cheetahs were almost identical, with median, mean and maximum distance of 0.012 km, 0.56 km and 15.30 km, respectively. Overall, they spent 82% of their time within 100 m of each other, although there were larger separations between them near the end of the observation period (Figure 2A-C). The cheetahs' home range (as proxied by C1) was 3 times larger (MCP: 1137.2 km^2) than that of the leopard (407.9 km^2), and the cheetahs' home range overlapped with 95% of PL home range in the overlapping time-frame (Figure 1C). During the intersecting observation period of all animals, the mean, and maximum of C1-PL distance were 12.2 km and 42.2 km, respectively. In the linear regression analysis, C1-PL distance was negatively associated with C1-C2 distance ($P<0.01$), indicating that closer proximity of the leopard was associated with greater distances between the cheetahs (Figure 3). However, C1-PL distance only explained 2% of the variations ($R^2=0.02$) in the C1-C2 distance. The Chi^2 contingency test of the C1 and PL movement behaviours at simultaneous points was not significant indicating their movement behaviours were independent of each other ($P=0.16$, Chi^2=1.97).

Elevation, slope, distance to the nearest water and distance to the nearest pathway were significant movement predictors for both animals ($P<0.05$) after fitting the RSF to individual animal tracks (Supplementary Data 1). However, the shape of the

Figure 4. Skull of an Asiatic Cheetah (C1) apparently killed by a leopard. The presence of distinct lateral and dorso-lateral perforations of the C1's skull, additional to the telemetry data, confirmed the leopard bite.

relationship (linear versus quadratic) differed between species and covariates. Both species were more likely to occur in mid-range elevations and slopes; however, the cheetah selected lower elevations and grounds with lower slopes than the leopard (peak RSF at 1629.3 m for C1 versus 2031.2 m for PL). Leopard occurrences exhibited a linear relationship with respect to human pathways, peaking at a distance of 4656 m. In contrast, the cheetah was more likely to stay at greater distances from pathways, peaking at 6527 m. The leopard chose locations closer to the water sources (2.3 ± SD 1.6 km) than the cheetah (3.5 ± SD 3.4 km). Interestingly, the pattern persisted for distances to the nearest highway with the leopard preferring shorter distances (12.3 ± SD 3.4 km) than the cheetah (14.5 ± SD 6.7 km).

Discussion

The dataset of a coalition of two Asiatic Cheetahs and one Persian Leopard obtained in this study is unique, as it documents the movements and interactions of rare felid predators, one of which falls prey to another. However, the data were limited by a relatively short time span of a few months and relatively coarse (8 h) temporal resolution as well limited number of individuals. Thus, a comprehensive and rigorous quantitative analysis relies on an integrated suite of GIS, habitat, and movement analysis tools. This study is the first such analysis of these two sub-species monitored concurrently.

The Persian Leopard tended to remain in the more montane central and northern parts of the Bafq Protected Area never coming closer than a few kilometres to the highways. Its habitat preferences agreed broadly with the range-wide analysis of Persian Leopard habitat use by Gavashelishvili and Lukarevskiy (2008), who indicate a global preference for relatively rugged and dry terrain with a strong avoidance of human presence and a local avoidance of low-productive areas, like low-lying deserts.

In Bafq, the presence of human infrastructure such as highways, cities, villages and pathways has made dispersal more difficult for large cats. The transportation network around the animals' home ranges (Figure 1A) has increased the risk of mortality through road accidents: at least seven cheetahs have died due to vehicle collisions in

Kalmand PA, 15-20 km west of Bafq Protected Area from 2007 to 2011 (Mohammadi & Kaboli, 2016). Although cheetahs also avoided highways, they ranged much more widely than the leopard throughout the Bafq region yet they remained at further distances to the human pathways and at lower elevations than those of the leopard. Cheetahs are less suited than leopards to higher elevations and may find other suitable prey in lower and flatter areas such as Chinkara and Cape Hares.

The leopard's distance to the cheetahs explained 2% of the variance in cheetahs' distance when separated. In a few occasions the closer the leopard was, the further apart the cheetahs were after mid-July. This is, perhaps, the indication of interactions, though it is impossible to determine whether it indicates that the cheetahs scattered as a response, or that the leopard approached when the coalition was weakened by separation. Once found, C1's abdomen was open and thoracoabdominal organs such as some parts of hind-limb muscles were missing. Leopards are known to kill and, in some cases, eat cheetahs elsewhere (Broekhuis, 2015), however, it is uncertain whether the leopard fed upon the carcass or if it was later scavenged by other species. The deadly encounter took place over a freshly killed Bezoar Goat suggesting that the cheetah death could have been the result of an interspecific competition over a natural prey.

Altogether, the avoidance of humans, pursuit of prey, the need for water and avoidance of top predators, collectively determined the movements of large cats in this study. The Bafq Protected Area seems to be a relatively good habitat for the leopard, while the situation appears to be more dire for the cheetah, which appears to be squeezed between conflicts with humans and a local apex predator, and therefore potentially relegated to suboptimal habitat in which it is more vulnerable to human pressures. The future conservation of the Asiatic Cheetah will depend on corridors linking a highly fragmented and dispersed population, as well as on expansion of wildlife reserves, including the Bafq Protected Area (Farhadinia et al., 2016; Moqanaki & Cushman, 2017).

Detailed modelling and analysis of habitat and interrelated movement behaviour of sympatric animal species are crucial to decipher their behavioural ecology. We identified a signal of detrimental interaction between the Persian Leopard and the Asiatic Cheetah, demonstrated for the first time that Persian Leopard killed Asiatic Cheetah, and identified the species' unique responses to environmental variables. A larger sample size would have led to more general and meaningful inferences on the behavioural ecology of the species; future work involving more individuals with overlapping ranges would clarify the species' interactions in Iran.

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Disclosure Statement

No potential conflict of interest was reported by the authors.

Supplementary Information

The code for analysing the spatial interrelationships of simultaneously tracked individuals, along with the data, are accessible at https://github.com/faridcher/cacpl.

- Supplementary Data S1: sd1.docx file that contains detailed tabular information on the movement and environmental data, and less significant results.
- Supplementary Data S2: sd2.kmz file for 3D visualization of the animal tracks along with their environmental covariates in the study area which can be opened with Google Earth application.
- Supplementary Data S3: sd3.mp4 file shows the simultaneous movement of the three cats as an animation movie in the study area; it is better to navigate it frame by frame at a desired speed using a media player for a meticulous exploration.

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