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Running Header: Predation patterns of Persian leopards

Persian leopard predation patterns and kill rates in the Iran-Turkmenistan borderland

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Describing predation patterns and especially estimating kill and consumption rates is essential

for understanding the functional responses of predators. An understanding of the carrying

capacity of the landscape, based on prey availability, also helps to formulate recovery plans for persecuted species. We studied the feeding behavior of the Persian leopard (*Panthera pardus saxicolor*) in Tandoureh National Park (355 km²) in northeastern Iran, near the Turkmenistan border. Between September 2014 and May 2017, we collared and monitored 6 adult leopards (5 males and 1 female) using GPS-satellite Iridium collars. We investigated 310 clusters of fixes as likely to be kill sites. In total, 130 kills were identified to species, suggesting a mean kill rate of approximately 3.3 ± 0.3 (SE) kills/month per adult male leopard, which is higher than reported by most previous studies. The leopards varied considerably in the time they spent outside the national park; only 1 individual appeared to subsist mainly by raiding livestock. The availability of medium-sized ungulates at adequate densities is likely to be important for future leopard conservation efforts. The management of problem individuals also may promote coexistence of humans and leopards, even in prey-rich areas.

Key words: conflict, kill rate, Persian leopard, predation behavior, prey choice, satellite telemetry

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Of the big cats, common leopards (*Panthera pardus*), have the broadest dietary requirements (Sandom et al. 2018), and are widely perceived to be generalist predators (Martins et al. 2011; Shehzad et al. 2015). Linked to that, they have flexible habitat requirements (Gavashelishvili and Lukarevskiy 2008). However, studies using fine-scale radio-tracking data have revealed that

leopard populations can show some degree of specialization in their choice of prey (Stander et al. 1997; Radloff and du Toit 2004) and hunting habitat (Balme et al. 2007).

The predatory behavior of leopards has been investigated across a range of habitat types using fecal analysis (see Stein and Hayssen 2013), spoor tracking (Bothma and le Riche 1982; Stander et al. 1997), direct sighting (Bothma and le Riche 1982; Balme et al. 2007), and telemetry (see Stein et al. 2015). There is consequently a wealth of knowledge on leopard diets for most of their global range.

The rates at which prey are killed and consumed are less well understood. Effective management of predator–prey systems largely depends on reliable estimates of these metrics (Knopff et al. 2010). As well as informing predator-prey dynamics (Wegge et al. 2009), they are likely to indicate the extent of conflict with local stockholders (Farhadinia et al. 2014b; Ghoddousi et al. 2016) and also allow estimation of the nutritional carrying capacity of an area (Hayward et al. 2007; Jooste et al. 2013). Detailed knowledge of predation patterns also can reveal individual dietary specialists, which are increasingly recognized as being widespread in predator populations (Lowrey et al. 2016). These attributes of predation are not straightforward to study. Problems with estimating components of predation in previous studies include tracking sessions that are too short (19 days; Odden and Wegge 2009), inadequate sampling of kill sites (Martins et al. 2011), delays in identifying kill sites due to time lapsing before downloading data (Stein et al. 2015), and failure to verify kill sites identified from clusters of movement fixes (Rozhnov et al. 2015).

The substantial variation in previous estimates of kill rates, from 1.5 prey items per month (based on VHF radio-telemetry; Hamilton 1981) up to 10 items per month (using spoor tracking;

Bothma and le Riche 1982) may reflect biological differences across the leopard's geographic range, methodological inadequacies, or both. To circumvent these problems, GPS telemetry has been recommended (Knopff et al. 2009; Elbroch et al. 2017). This approach requires that fix success, which is defined as the proportion of all scheduled fix attempts that are successful is > 45% (Knopff et al. 2009) and that predation sequences are continuously monitored in the field over long periods (Laundré 2005).

The endangered Persian leopard (*P. p. saxicolor*) currently exists in only 16% of its former range in west and central Asia (Jacobson et al. 2016). Its prey has been documented to vary from rodents to domestic cattle and horses (Taghdisi et al. 2013; Ghoddousi et al. 2016; Sharbafi et al. 2016b). However, rigorous quantification of predation patterns are sparse for leopards in Asian montane landscapes (Wegge et al. 2009). This is especially pertinent for the Persian subspecies whose natural prey is being depleted across west and central Asia (Farhadinia et al. 2014b).

In this paper, we used GPS data to address 4 objectives concerning the predation patterns and foraging behavior of Persian leopards, the apex predator in Tandoureh National Park (NP) along the Iran-Turkmenistan borderland. First, we explored leopard prey choice and how it is affected by spatiotemporal factors. Second, we quantified kill rates (number of prey per individual per month) and then converted kill rates to estimates of consumption rates. This information is particularly important where prey species are trophy hunted, as is the case around Tandoureh NP and other mountainous reserves. We also explored inter-kill intervals and handling times, hypothesizing that larger prey body mass would require greater handling time and be followed by longer inter-kill intervals compared with smaller prey items.

MATERIALS AND METHODS

Study area.— Tandoureh NP in north-eastern Iran (ca. 20 km from the Turkmenistan border) has been protected since 1968 and covers 355 km². It is characterized by mountains populated with wormwood (*Artemisia* sp.) and scattered juniper trees (*Juniperus* sp.). Elevation ranges from 1,000 to 2,600 m. Human settlements, most of which are associated with sheep and goat herds, border the park. Potential wild ungulate prey for leopards is limited to urials (*Ovis orientalis*), bezoar goats (*Capra aegagrus*), and wild pigs (*Sus scrofa*), which all are subject to occasional trophy hunting in the mountainous terrain surrounding the national park.

The availability of leopard prey in Tandoureh NP is affected by the national park boundaries. Wild bovids occur almost entirely inside the park, wild pigs occur throughout both areas but at reduced densities outside the park, and domestic animals such as sheep (*Ovis aries*), goats (*Capra hircus*), and domestic dogs (*Canis familiaris*) are found almost exclusively outside the park across multi-use lands.

Leopard capturing and collaring.— We captured leopards with Aldrich foot-snares modified extensively to reduce the chance of injury (Frank et al. 2003). Traps were fitted with remotely monitored VHF transmitters (Wildlife Materials, Inc., Carbondale, Illinois) emitting signals every 1-2 hours (see Farhadinia et al. 2017 for more details). As leopards are known to respond to baits (du Preez et al. 2014), a wild pig carcass was used as bait, normally hanging from a tree or rock. Traps also were deployed along trails leading to the baits. In summer, we deployed traps along trails leading to water sources, sometimes without bait (see Farhadinia et al. 2017 for more details).

We immobilized leopards using a combination of ketamine 10% (Alfasan, Nederland BV) 2 mg/kg, medetomidine HCl 20 mg/ml (Kyron Laboratories (Pety) Ltd., Johannesburg, South

108 Africa) 30 µg/kg and butorphanol 0.2 mg/kg (Torbugesic®, Fort Dodge Animal Health, Fort
109 Dodge, Iowa) delivered intramuscularly with a dart gun (Daninject, Børkop, Denmark) using a
110 1.5 ml dart.

111 We used GPS collars with Iridium download (LOTEK Engineering Ltd., Newmarket, Ontario,
112 Canada). Each collar incorporated a drop-off buckle with a timer set to 52 weeks post-
113 deployment. Collars weighed 640 g, equivalent to less than 1-2% of leopard body mass. Each
114 animal's age was estimated based on dentition (Stander 1997). Anesthesia lasted for between 44
115 and 60 minutes, followed by reversal using atipamazole (3 times the medetomidine dosage) and
116 nantroxan (the doses equal to butorphanole), injected intramuscularly.

117 Capture and handling of leopards followed the guidelines of the American Society of
118 Mammalogists (Sikes 2016). The Iranian Department of Environment reviewed and approved all
119 sampling, trapping and handling procedures (research permit number 93/16270). The trapping
120 and handling protocol was also approved by University of Oxford's Ethical Review Committee
121 (BMS-ERC-160614).

Cluster investigation.— We followed Knopff et al. (2009) who recommended recording fixes every 3 hours to enable the identification of spatially aggregated GPS points, or clusters, while ensuring the survival of transmitters batteries for at least 1 year. This was based on a study of cougars (*Puma concolor*) feeding on prey > 8 kg. Collars were programmed with a ‘virtual fence’ option triggering an increased fix rate, to hourly, when leopards left the park. This enabled us to detect kills reliably outside the national park where prey generally have a smaller body mass (i.e., domestic animals) and scavengers, such as herding and stray dogs, golden jackals (*Canis aureus*), and striped hyenas (*Hyaena hyaena*) are more abundant.

Initially, clusters were defined as ≥ 2 locations within 100 m of each other and with the earliest and latest location separated by less than 12 hours (Knopff et al. 2009; Martins et al. 2011; Johansson et al. 2015). Handling time and cluster fidelity are 2 predictors of kill clusters (Knopff et al. 2009; Martins et al. 2011), but clusters using only daytime locations yielded remains of prey at only 2 locations (2 bezoar goats in 36 visits).

To determine the timing of feeding, we deployed Bushnell Trophy Cam camera traps (Bushnell Outdoor Products, Overland Park, Kansas) at fresh kills or baits ($n = 14$) in northeastern Iran. This revealed that both male and female leopards remained on kills overnight (6 urials, 2 wild pigs, and 6 dogs), with the exception of 1 occasion when a female and cub did not return to their kill after deployment of the camera trap. Our observations supported the conclusion that leopards predominantly feed at night (Stander et al. 1997). As a result, in accordance with Johansson et al. (2015), we considered daytime clusters to be rest sites. Therefore, GPS clusters where leopards remained overnight (between 18:00 and 06:00 h) within a radius of 200 meters were investigated for possible kill remains. Nonetheless, we acknowledge that we may have missed small prey, especially if they were consumed during daylight.

We identified clusters visually using Google Earth 5 (Google Corporation 2009) and a web-based map-system for displaying telemetry data (webservice.lotek.com) in a 6-8 day time-frame. Distances between each consecutive GPS locations were calculated. Candidate GPS cluster locations were then uploaded on a hand-held GPS device (Garmin GPS62S, Garmin International, Olathe, Kansas) to enable ground crews of ≥ 2 people to systematically search within a radius of at least 100 meters from each cluster location for at least 20 minutes, following (Knopff et al. 2009).

Prey remains were thoroughly investigated to identify prey species, and where this was uncertain, hair samples were taken for lab investigation based on a reference hair collection (Rezaei 2014). We used horn size and annual growth rings to assign sex and age to bezoar goats and urials. Additionally, long white hairs of adult urial rams were diagnostic of sex. Age categories were defined as adult (> 4 years old), young (> 1 and $4 \leq$ years old), and lamb ($1 \leq$ year old).

Cluster locations were visited over 87 days between September 2014 and May 2017. Twelve locations were discarded as not being accessible because of extreme weather conditions at high elevations, leaving a total of 310 locations that were investigated as candidate clusters (Table 1). Cluster sites were visited only after at least 2 days had elapsed since the leopard's last location at the site. In the dry montane landscape, hair, horns, bone pieces, etc., can be detected several months after a kill (Johansson et al. 2015). We included only kills found within 120 days of the identification of a cluster to estimate the consumption rate. We split monitoring time into multiple sampling periods in which we visited every cluster to avoid bias caused by inclusion of non-investigated clusters.

Prey characteristics.— Prey species were allocated to 2 size categories. The “small” prey (< 15 kg) included red foxes (*Vulpes vulpes*), Indian crested porcupines (*Hystrix indica*), and birds. The “medium” prey (≥ 15 kg) category included urials, bezoar goats, wild pigs, domestic sheep, and domestic dogs. Young wild ungulates and domestic animals also were included in medium-sized prey.

In Tandoureh, prey availability differs markedly on either side of the national park boundary. Thus, to understand patterns of predation on wild (inside the NP) versus domestic medium-sized prey (outside NP), we calculated the time (days) each leopard spent either inside or outside the national park as a proxy for livestock versus wild prey spatiotemporal availability.

For those medium-size prey for which sex was determined (i.e., urial and bezoar goats), contingency-table-based chi-square tests also were used to explore sex-biased selection. Sex ratios were based on observations of seasonal prey count surveys along transects laid within the national park, usually along ridgelines or valley bottoms. The time, location, and sex and age structure (using 12×42 binoculars and 20-60 telescope) of all urial and bezoar goat sightings were recorded. Transects, varying in length between 5 and 26 km, were laid at least 3 km apart in order to avoid double-counting. In total, 247 km of transects were surveyed between August 2013 and March 2015. Although there was partial temporal overlap between our prey survey and cluster investigations (September 2014– May 2017), there was no evidence of any major variation in the prey populations during this period. Therefore, we are confident that the estimates of ungulate population demographics can be compared with our exploration of predation based on the location of clusters.

To minimize misidentification of different sex and age groups, we excluded all sightings further than 700 m from the center line of each transect. Distances were measured using a Nikon

Monarch Gold Laser1200 Long Range Rangefinder (Nikon Inc., New York, New York). We improved the accuracy of urial and bezoar goat detection at the sex and age level using images taken with a digital zoom cameras (Nikon P500 36X optical zoom or Fuji Finepix S1 50X optical zoom). For better identification of age classes based on size and shape of horns, images of urials and bezoar goats were investigated on a computer and thus the proportion of individuals within each sex and age class category was calculated. We then used Fisher's exact test to test if prey age was independent of leopard age. Each age was defined as either young (< 4) or adult (≥ 4) for leopards.

To explore prey choice, we used mixed effects cumulative link models for the analysis of nominal responses. Multinomial models were fitted using the 'Mixcat' package in R (Papageorgiou and Hinde 2012). Each prey type was treated as a nominal response variable. Predictor variables included season (4 seasons), the time since leaving the last kill (last fix at radius of 200 meters of where the prey was found), as well as last meal size (kg). To account for individual variability in prey choice, leopard ID was assigned as a random effect which was about the minimum number (6 levels) required for obtaining reliable estimates for random effects terms (Bates 2010).

Seasons were defined as March to May = spring, June to August = summer, September to November = autumn, December to February = winter. The significance of terms in the final model was assessed using log-likelihood ratio tests for comparing the goodness of fit between models.

Kill and consumption rates.— Topography and animal behavior can influence the performance of GPS telemetry collars, including fix success rates, which results in missing data (Cain III et al. 2005). Although our overall fix rate was high (mean 85.0% \pm SE 7.6), we removed kill intervals containing overnight fix failures ($n = 9$) before analysis (either unsuccessful or non-retrieved fixes). Prey scavenged by leopards ($n = 9$), small prey ($n = 9$) and those found after 4 months ($n = 21$) also were excluded from calculations of kill rate. In total, 91 medium-sized prey remains were used to estimate kill rates for medium-sized prey.

We used a ratio estimator (Hebblewhite et al. 2003), which truncates the denominator to the period between the first and last kills of each sampling period. We used total monitoring time (as a cumulative of all sampling periods) as the denominator for rate estimation and both number of kills and kilograms of prey as numerators, yielding frequency (kills/month) and biomass (kg/day) metrics for each individual (Knopff et al. 2010; Miller et al. 2013). We acknowledge that we estimated the potential maximum consumption rate of detected kills, because we assume that all edible parts of each kill are consumed by the leopards.

To calculate biomass consumed by the leopards, we assigned approximate live weights to prey, using values from the literature or from measurements made in northeastern Iran. Weight estimates for adult female and young male urials were obtained from Valdez et al. (1977) while weight measurements were collated for adult male urials ($n = 10$), all age and sex categories of bezoar goats ($n = 11$), red foxes ($n = 8$), domestic sheep ($n = 3$), and domestic dogs ($n = 2$), all from intact carcasses found in the field. We were not able to identify the sex of the wild pigs and porcupines, so species-level average body mass were obtained from Goshtasb (2001) and Mori and Lovari (2014), respectively.

We weighed the horns of male urials and bezoar goats (both adult and young) and subtracted their weight from mean body mass. Then, we used regression to calculate the non-consumable portion of a prey carcass typical for big cats (Fàbregas et al. 2017). We concluded that 22% was non-edible for bezoar goats and urials, 25% for wild pigs, 21% for domestic dogs, 23% for domestic sheep, 16% for Indian crested porcupines, and 12% for red foxes.

We found no evidence for non-trivial rates of domestic animal raiding around Tandoureh using our questionnaire surveys (Farhadinia et al. 2017). Thus, in order to calculate monthly predation rates for each prey species, we omitted data from leopard M1, because of his unusually high rate of depredation on domestic stock.

Patterns of hunting behavior.— Leopards are known to drag their kills to a concealed location before consumption; Stander et al. (1997) recorded an average distance of 140 m from the kill site. Thus, to calculate time of day when the leopard hunted, denoted as ‘predation time’, we estimated the earliest time for locations within 200 m of each kill cluster centroid. ‘Handling time’, defined as amount of time a leopard spent on a kill, was calculated as the time difference between first and last times locations were recorded within this radius (Knopff et al. 2010). If the leopard wandered outside the kill area, that time was subtracted from the handling time. We also estimated ‘inter-kill interval’ as the time period between 2 consecutive predation times. Finally, ‘search time’ was calculated as the inter-kill interval with handling time subtracted, i.e., the time elapsed since leaving the last meal and making the next kill (Hebblewhite et al. 2003; Knopff et al. 2010).

We developed a generalized linear model to relate a handling time response to kill location (inside or outside Tandoureh) and last prey weight. Another set of generalized linear models also

were constructed to explore how season, location, and last prey weight (kg) were associated with a response defined as inter-kill interval. Finally, we modelled the effect of season on kill rate and consumption rate of leopards. Leopard ID was treated as a blocking factor in all modeling attempts. Response variables were square-root transformed, because model diagnostics were more compatible with distributional assumptions comparing to non-transformed and log-transformed data. Model selection for inter-kill interval was performed using corrected Akaike Information Criteria (AICc), using the ‘AICcmodavg’ package (Mazerolle 2011). All means are reported with standard errors. We conducted all analyses in R (R Development Core Team 2013).

RESULTS

Between September 2014 and May 2017, 6 leopards (5 males and 1 female) were collared and monitored in and around Tandoureh, comprising 4 adults and 2 young individuals (Fig. 1). Their kills were monitored for 1,554 leopard-days (mean = 259.0 ± 52.6 days/leopard, Table 1). The leopards varied considerably in the time spent outside the national park within multi-use areas (in total, 17.9 ± 7.3 % of tracking days overall, varying between 0.0 and 43.8% for different individuals). Field signs confirmed that the leopards scavenged 9 times (varying between 0 and 4 events among individuals), mostly at baits we deployed for capturing and collaring operations (Table 1). Four clusters were excluded because of mismatches between dates of the cluster and the age of the kill found there.

Prey characteristics.— We found 130 prey items of 10 species that we assigned to 3 categories (Fig. 1; Table 1): wild ungulates (urials, bezoar goats, and wild pigs), domestic animals (dogs, sheep), and small animals, such as Indian crested porcupines, red foxes, raptors, pigeons (*Columba livia*), and chukar partridges (*Alectoris chukar*). Domestic prey were killed exclusively outside the national park, whereas 96.6% of all wild ungulate kills were within the park (Fig. 1). Non-domestic kills outside the park were urials ($n = 3$), wild pigs ($n = 2$), small mammals, and birds (Fig. 1). There was no evidence that prey type was influenced by season, the weight of the last prey item, or the search time since last kill (Table 2).

The majority of prey items were medium-sized species, with small animals comprising only a small minority (93.3% medium-sized versus 6.7% small; Table 3). Although wild prey dominated leopard diet (81.5% wild versus 18.5% domestic animals; Table 3), there was no evidence that the frequency of prey types (wild versus domestic animals) was out of proportion with the amount of time that leopards spent inside or outside the national park ($X^2_1 = 0.01$, $P = 0.92$). Amongst individual leopards, there was a strong positive correlation between the proportion of time each spent outside the national park and the percentage of kills each made of domestic stock ($r_s = 2.06$, $P = 0.005$). Although domestic animals were not detected in the clusters investigated for 3 individuals, they comprised 46.2% of medium-sized kills made by an old male (M1; Table 1).

A total of 176 groups of urials and bezoar goats were detected, but 31 were excluded as their distance did not allow us to identify their age and sex composition. Consequently, 1,875 individual urials (100 detections) and 918 bezoar goats (45 detections) were recorded (Supplementary Data SD1). In urials, 90.0% of young males were detected in maternal groups, whereas 69.9% of young male bezoar goats were spotted in such mixed groups. A grand mean

ratio of 40.7 (\pm 7.5) adult rams was calculated per 100 urial ewes, whereas there were 40.6 (\pm 0.4) adult males per 100 female bezoar goats. Of 95 kills of urials and bezoar goats (73.1% of the total; Table 1), 87.1% were males versus 12.9% females, 80.8% were adults versus 19.2% young or lambs. The observed male-biased predation was statistically significant for both urials and bezoar goats ($X^2_1 = 54.0$, $P < 0.005$, and $X^2_1 = 72.4$, $P < 0.005$, respectively). Young leopards killed both young and adult prey equally (50.0% adult versus 50.0% young), whereas adult leopards killed a preponderance of adult prey (88.1% adult versus 11.9% young; Fisher's exact test, $P = 0.003$). Adult male urials and bezoar goats killed by the leopards were on average 7.1 ± 0.4 and 6.9 ± 0.3 years old. Four of 6 wild pig remains were young adults (< 2 years).

Kill and consumption rates.— The only collared female leopard (F5) consumed 127.5 kg of edible prey during 54 tracking days, amounting to 2.4 kg/day. For males, we estimated a rate of 3.3 ± 0.3 kills/month, equal to a daily rate of 0.11 ± 0.01 kill. Kill rates varied substantially among individuals (range 2.2–4.1 medium size prey/month and 2.9–5.5 kg/day; Table 1). Each adult male leopard consumed an average of 129.6 ± 2.0 kg/month, i.e., 4.3 ± 0.1 kg daily (Table 1), equivalent to an average of 40.0 ± 3.9 medium-sized prey per annum ($1,554.8 \pm 24.6$ kg of medium-sized edible biomass). There was no evidence for seasonal variation in either kill rate ($F_{3,8} = 1.01$, $P = 0.44$; Fig. 2a) or consumption rate ($F_{3,8} = 1.58$, $P = 0.27$; Fig. 2b). On 3 occasions, a cluster revealed 2 prey (cases 1 and 2 for leopard M1: wild pig and urial, dog and domestic sheep; case 3 for M4: urial and red fox). Additionally, M1 killed 2 dogs at the same time, of which he carried off only 1.

Patterns of hunting behavior.— The leopards spent an average of 51.9 ± 2.9 hours at each kill. At 30.1% of the kills, leopards spent some time moving beyond the feeding area (3.0 ± 1.0 hours), to which they intermittently returned. Handling time (time spent at a kill) was not

correlated with prey body mass ($r^2 = 0.38$, $P = 0.71$). There was no evidence that the prey weight ($F_{1, 96} = 0.01$, $P = 0.94$) or whether the kill occurred inside or outside the park ($F_{1, 95} = 0.61$, $P = 0.43$) affected handling time in a cluster.

There was no evidence that the inter-kill intervals were usefully predicted by any of the modelled variables (the best performing model was the null, including only leopard ID; Table 4). Summer inter-kill intervals were shortest (6.7 ± 1.2 days; $F_{3, 90} = 1.82$, $P = 0.15$; Fig. 2c). In total, 50.0% ($n = 11$) of summer kills within the national park were within a kilometer distance of the nearest water resource.

DISCUSSION

We observed a kill rate higher than most previously published estimates for leopards. Wild ungulates were the principal prey. Leopards showed age-dependent selectivity for certain prey age and sex groups. A single individual relied mainly on domestic stock, whereas others predominantly killed wild ungulates.

Prey characteristics.— Young leopards preyed mainly on young wild ungulates whereas adult individuals predominantly hunted adult ungulates. Prey body mass, a key predictor of prey selection, may explain this selective foraging by different ages (Radloff and du Toit 2004; Knopff et al. 2010; Elbroch et al. 2017).

Leopard populations are known to show some degree of specialization in their choice of prey (Stander et al. 1997) or hunting habitat (Balme et al. 2007). Our data revealed selective hunting of adult male (> 4 years) urials and bezoar goats. There are few previous observations of sexual selectivity by leopards. Owen-Smith (2008) observed an excess of female impala (*Aepyceros melampus*) in leopard diets, but males are more commonly targeted (Bailey 1993; Karanth and

Sunquist 1995). Anti-predator vigilance, which is more common in females and kids among mountainous wild sheep and goats (Cransac et al. 1998; Grignolio et al. 2007), is a possible explanation for apparent male-selective predation by Persian leopards. Similarly, the majority of young males of both principal prey species, i.e., urials and bezoar goats, observed in Tandoureh were accompanied by maternal groups, which may provide some defense against predators. Predator populations may be an aggregate of individual dietary specialists (Bolnick et al. 2002); dietary variation possibly reflects differences among individuals in foraging behavior rather than prey availability (Lowrey et al. 2016). Future research should therefore address individual variation in predatory behavior.

Previous studies on diets of Persian leopards in northeastern Iran based on fecal analysis (Taghdisi et al. 2013; Farhadinia et al. 2014b; Ghoddousi et al. 2016; Sharbafi et al. 2016a) have shown consistent dominance of wild ungulates in the diet, estimated to constitute 80-95% of consumed biomass. We acknowledge that our measure of spatial availability of domestic animals could have benefited from incorporating the density of domestic versus wild prey. Nonetheless, the taking of domestic animals in Tandoureh was closely associated with the amount of time individuals spent in multi-use areas, i.e., outside the NP. Therefore, dietary analysis based on fecal sampling within livestock-free national parks might underestimate stock raiding by leopard individuals, which generally happens outside the national parks. The minor role for domestic stock consumption (5-20%) recorded in previous studies may also be an underestimate, not reflecting stock predation and defecation in excursions beyond the national park boundary. Our data showed that even though most individuals had access to domestic stock when making periodic excursions in human-dominated landscapes outside the national park, only 1 leopard (the old male M1) regularly targeted the stock of local communities.

Our findings have some limitations. First, they are based on a limited sample of GPS-collared leopards, and mostly males. Second, our data were restricted to larger prey items associated with clusters of fixes. All small prey items were detected along the Tabdoureh boundary or outside (Fig. 1), where the ‘virtual fence’ technology shifted the fix interval from every 3 hours to hourly. The longer fix interval reduced the likelihood of detecting smaller prey items inside Tandoureh. In contrast, our variable fix interval was unlikely to affect identification of medium-sized prey because the leopards spent on average 2 days at a kill, clearly long enough to detect a cluster. We could not assess the extent of predation on small-bodied prey (rodents, lagomorphs, and birds) that are unlikely to generate GPS clusters with our fix programming inside Tandoureh (Knopff et al. 2010). However, various fecal analyses revealed negligible consumption of small animals in northeastern Iran (Taghdisi et al. 2013; Ghoddousi et al. 2016). Third, young wild ungulates, particularly lambs, are likely to have been underrepresented in our kill data, because their small body size and delicate skeletons make them easy to consume rapidly, such that no cluster of fixes results. Large cats often show a seasonal shift to neonates after ungulate birth pulses (Owen-Smith 2008; Knopff et al. 2010). To explore the seasonal shift hypothesis, future studies would need to use shorter fix intervals (≤ 1 hour).

Kill and consumption rates.— Our estimate of kill rate was higher than reported in most previous studies (Table 5). This is likely to be due to both methodological and ecological factors. Leopards vary markedly in size across their range. The Persian leopard is one of the largest subspecies (Stein and Hayssen 2013), adult males weigh on average 65.8 kg (Farhadinia et al. 2014a). Higher mass-related energetic requirements may therefore at least partly explain the higher consumption rate (Carbone et al. 1999).

The majority of previous estimates (Table 5) are based on studies with limitations of some kind. In some, the leopards were tracked for relatively short periods (Odden and Wegge 2009); in others, small to large prey were included in the calculation (Bothma and le Riche 1982), or some potential kills were neglected (Martins et al. 2011; Rozhnov et al. 2015). Similarly, relatively high kill rates were reported for Amur tigers (*P. tigris altaica*— Miller et al. 2013) and cougars (Knopff et al. 2010) when GPS clusters were used compared with estimates derived from other techniques.

Our data revealed that estimates of kill rate varied almost 2.5-fold among individual leopards. Similar individual variation has been reported from other cats, such as jaguars (*P. onca*— Cavalcanti and Gese 2010), cougars (Knopff et al. 2010), and tigers (Miller et al. 2013). The lowest kill rate (by an adult male, M3) was associated with a home range in the eastern margins of Tandoureh where prey density was thought to be low.

Patterns of hunting behavior.— Large felids tend to stay longer on larger kills where wider ranges of prey sizes are available (Cavalcanti and Gese 2010; Knopff et al. 2010; Miller et al. 2013). The amount of time a leopard spent on a kill was not associated with either body mass of the prey or location (inside or outside the NP). The limited range of prey size in Tandoureh (medium-sized mammals) may account for the lack of variation in handling time. Likewise, assigning kills to either inside or outside the NP may have not captured the necessary spatial scale at which distinct behaviors are affected by human interference outside the national park (Wilmers et al. 2013). We did observe that all kills made outside the NP were dragged to nearby rocky cliffs and mountains, a behavioral response to avoid human interference. Therefore, the available landscape heterogeneity in these multi-use landscapes may provide sufficient cover for leopards to avoid the fear induced by humans (Smith et al. 2015).

Our data showed no evidence for seasonal differences in kill rate and predation patterns in Tandoureh. In contrast, seasonal predation pattern is widely reported in big cats, explained by migratory prey species, synchronized birth pulse in prey and changes in environmental situations or predator energetic requirements (Cavalcanti and Gese 2010; Knopff et al. 2010; Miller et al. 2013; Allen et al. 2014). In Tandoureh, the ranging patterns of the principal prey species, i.e., urials and bezoar goats, are mainly dictated by the national park boundary. Pastures outside the national park are occupied by herds of livestock with limited water availability. In the north, the park is surrounded by open farmlands while 2 roads delineate the park perimeter to the west and east. Seasonal migration would not therefore be likely to benefit wild ungulates.

The shortest inter-kill intervals were observed in summer. There are two possible explanations. First, in summer there are abundant vulnerable juvenile ungulates just after their birth pulse in spring (Laundré 2008). No depredated lambs were, however, found in summer. Alternatively, the shorter observed intervals in summer for medium-sized prey could be explained by the ease of hunting ungulates around scarce water resources; one-half of summer kills were found near water resources.

Management implications.— Our observations suggest, albeit tentatively given the low number of individuals observed, that domestic animals, even in areas where wild prey is abundant, can comprise a substantial part of leopard diets. It is also clear that stock-raiding behavior may be confined to problem individuals rather than being a characteristic of the entire population. In general, problem individuals can be responsible for a disproportionate impact on human interests, such as health, culture, well-being, and economics (Swan et al. 2017). Selective management targeting specific individuals can therefore be effective in conflict mitigation (Linnell et al. 1999). Hitherto, translocation of problem leopards has often been favored, but the

effectiveness of this is not well established (Weilenmann et al. 2011; Odden et al. 2014; Weise et al. 2015). As such, any attempt at translocating problem individuals should be conducted under validated guidelines (Weise et al. 2015).

While leopards tend to be opportunistic predators, they do show a level of prey selectivity that should be taken into account where their prey species are exploited, for example by trophy hunting. Both leopards and trophy hunters select large male ungulates. If both trophy hunting of prey and leopard existence are to be sustainable, the number and spatial configuration of trophy quotas should be based on a sound evidence base; prey numbers should therefore be monitored.

Finally, our findings provide an empirical baseline for predicting the prey requirements of leopards and functional response of leopards, which couples their intake rate to prey density. We also highlight the need for protecting prey population as a key component of leopard conservation. As change in land use is the main threat for the ranges of threatened mammalian carnivores (Di Minin et al. 2016), we recommend that future studies focus on understanding the energetic requirements of leopards in areas where they increasingly share the landscape with human communities.

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SUPPLEMENTARY DATA

Supplementary Data SD1.— Details of urials and bezoar goats detected during prey surveys between August 2013 and March 2015 in Tandoureh National Park, northeastern Iran.

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FIGURE LEGENDS

Fig. 1. Distribution of all Persian leopard (*Panthera pardus saxicolor*) kill sites located inside and outside Tandoureh National Park, Iran from 2014 to 2017. Each polygon represents a collared leopard's 100% minimum convex polygon. Domestic prey were confined to areas outside the national park. In contrast, wild ungulates were predominantly killed within the park boundaries.

Fig. 2. Seasonal differences in predation patterns of Persian leopards (*Panthera pardus saxicolor*) in Tandoureh National Park, Iran (2014-2017). Error bars represent standard errors.

641 Table 1.— Summary of data used for estimating kill rates and potential consumption rate of Persian leopards (*Panthera pardus*
642 *saxicolor*) in Tandoureh National Park, Iran from 2014 to 2017.

| Leopard ID | Sex/Age | No. tracking days (days outside NP) | No. clusters searched | No. scavenges | No. kills | Prey species | | | | | | | | | | Kill rate (kill/month) ^d | Consumption rate (kg/day) |
|------------|---------|-------------------------------------|-----------------------|---------------|-----------|--------------|-------------|----------|-------|-----|-----------|-----|--------|--------|--------|-------------------------------------|---------------------------|
| | | | | | | Urial | Bezoar goat | Wild pig | Sheep | Dog | Porcupine | Fox | Raptor | Chukar | Pigeon | | |
| M1 | M/+10 | 368 (161) | 106 | 4 | 43 | 17 | 3 | 1 | 4 | 14 | 1 | 1 | 0 | 1 | 1 | 3.7 (0.7) | 4.4 (0.1) |
| M2 | M/7-10 | 362 (0) | 70 | 1 | 28 | 5 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3.4 (0.6) | 4.5 (0.1) |
| M3 | M/4-6 | 364 (49) | 57 | 0 | 21 | 11 | 5 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 2.2 (0.6) | 2.9 (0.1) |
| M4 | M/7-10 | 228 (5) ^a | 29 | 0 | 20 | 13 | 6 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3.9 (1.0) | 5.4 (0.2) |
| F5 | F/2-3 | 54 (4) ^b | 17 | 3 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | NA | NA |
| M6 | M/3-4 | 178 (59) ^c | 31 | 1 | 16 | 9 | 1 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 4.1 (1.2) | 5.5 (0.3) |
| Total | | 1554 (278) | 310 | 9 | 130 | 57 | 38 | 6 | 5 | 15 | 2 | 3 | 2 | 1 | 1 | 3.3(0.3) | 4.3(0.1) |

643 ^a The collar stopped functioning on 1 April 2017, probably due to battery failure. The animal was spotted again on 3 June 2017 with
644 the collar.

645 ^b Killed by a larger conspecific on 29 January 2016. We do not report its consumption rate due to small sample size of feeding events.

646 ^c M6 was collared for 326 days, but only 178 days spent within Iranian territory where we were able to closely monitor predation
647 behavior of the animal. On 29 February 2016, he left Iran for Turkmenistan.

648 ^d 91 medium-sized prey remains were used to estimate kill rate, after exclusion of prey scavenged by leopards ($n = 9$), small prey ($n =$
649 9) and those found after 4 months ($n = 21$).

650 Table 2.— Result of sequential likelihood ratio tests of multinomial models testing the effect of season, last prey weight, or search
651 time since last kill on prey type. LR stat. denotes likelihood ratio statistic (difference of residual deviance).

| Model no. | Explanatory variables | Test | DF | LR stat. | <i>P</i> |
|-----------|-----------------------|---------|----|----------|----------|
| 1 | Null | NA | NA | 274.9 | NA |
| 2 | Season | 2 vs. 1 | 3 | 273.8 | 0.76 |
| 3 | Search time | 3 vs. 1 | 1 | 274.5 | 0.51 |
| 4 | Last prey weight | 4 vs. 1 | 1 | 273.9 | 0.96 |

652

653

654 Table 3.— Prey species located at Persian leopard (*Panthera pardus saxicolor*) cluster kill sites (2014-2017) and their predation rate
 655 in Tandoureh National Park, Iran.

656

| Prey species | No. kills located | % total kills | % biomass | Kills/month (<i>SE</i>) |
|--|-------------------|---------------|-----------|---------------------------|
| Urial (<i>Ovis orientalis</i>) | 57 | 43.8 | 43.5 | 2.08 (0.75) |
| Bezoar goat (<i>Capra aegagrus</i>) | 38 | 29.2 | 36.2 | 1.14 (0.51) |
| Wild pig (<i>Sus scrofa</i>) | 6 | 4.6 | 7.8 | 0.24 (0.16) |
| Domestic sheep (<i>Ovis aries</i>) | 5 | 3.8 | 4.5 | 0.03 (0.03) |
| Domestic dog (<i>Canis familiaris</i>) | 15 | 11.5 | 8.0 | 0.09 (0.09) |
| Indian crested porcupine (<i>Hystrix indica</i>) | 2 | 1.5 | | |
| Red fox (<i>Vulpes vulpes</i>) | 3 | 2.3 | | |
| Birds | 4 | 3.1 | | |
| Total | 130 | | | |

657

658 Table 4.— Results of generalized linear model to explore effect of different predictors on inter-kill intervals (IKI) of Persian leopards
659 (*Panthera pardus saxicolor*) in Tandoureh National Park, Iran from 2014 to 2017. K = number of estimable parameters in the model,
660 ΔAICc = difference between model AICc and lowest AICc in the model set, AICc weight = Akaike model weight.

| Model number | Model | K | ΔAICc | AICc weight | Cum. AICc weight |
|--------------|--|---|---------------------|----------------|---------------------|
| 1 | IKI ~ LeopardID | 1 | 0 | 0.40 | 0.40 |
| 2 | IKI ~ LeopardID + Last prey weight | 2 | 0.8 | 0.27 | 0.66 |
| 3 | IKI ~ LeopardID + Location | 2 | 2.3 | 0.12 | 0.79 |
| 4 | IKI ~ LeopardID + Last prey weight + Location | 3 | 3.2 | 0.08 | 0.87 |
| 5 | IKI ~ LeopardID + Season | 2 | 3.4 | 0.07 | 0.94 |
| 6 | IKI ~ LeopardID + Last prey weight + Season | 3 | 5.0 | 0.03 | 0.97 |
| 7 | IKI ~ LeopardID + Location + Season | 3 | 5.9 | 0.02 | 0.99 |
| 8 | IKI ~ LeopardID + Last prey weight + Location + Season | 4 | 7.7 | 0.01 | 1.00 |

661

662 Table 5.— A review of comparative kill rates and food consumption rates of leopards (*Panthera pardus*) at different study sites, based
663 on different monitoring techniques.

664

| Habitat and location | Method | Kill rates (kill/month \pm <i>SE</i>) | | | Consumption rates (kg/day \pm <i>SE</i>) | | | Study |
|----------------------------------|-------------------------------|--|--------|-----------------|---|---------------|-----------------|----------------------------|
| | | Male | Female | Female with cub | Male | Female | Female with cub | |
| Semi-arid savannah, South Africa | Spoor tracking | 9.1 | | 20 | 3.5 | | 4.9 | Bothma and le Riche (1982) |
| Woodland savannah South Africa | VHF collar | 4.2 | 4 | | | 4.4–4.7 | | Bailey (1993) |
| Tsavo National Park, Kenya | VHF collar | 1.5 | | | | | | Hamilton (1981) |
| Meru National Park, Kenya | VHF collar | 2.3 | | | | | | Hamilton (1981) |
| Semi-arid savannah, Namibia | VHF collar and spoor tracking | 3.1-3.3 | 1.6 | 2.4-2.5 | 3.1–3.3 | 1.6 \pm 0.5 | 2.6 \pm 0.5 | Stander et al. (1997) |
| Temperate mountains, | GPS Argos | | 2.4 | | | | | Rozhnov et al. (2015) |

| | | | | | | | |
|-----------------------------------|-------------------------|---------|-----|-----|---------|---------|------------------------|
| Russian Far East | collar ^a | | | | | | |
| Subtropical forest, Nepal | VHF collar | | | 2.8 | 4.3±1.1 | 4.0±0.3 | Odden and Wegge (2009) |
| Woodland savannah, Botswana | GPS collar | 3.3 | 3.4 | 3.0 | | | Stein et al. (2015) |
| Open rocky mountain, South Africa | GPS collar ^b | 2.3 | 2.0 | | | | Martins et al. (2011) |
| Steppe mountain, Iran | Iridium-GPS collar | 3.3±0.3 | | | 4.3±0.1 | | This study |

665 ^a Potential kills were estimated based on cluster of GPS fixes, but were not visited in the field.

666 ^b Candidate clusters were partially verified in the field.