

Why do Amur tigers maintain exclusive home ranges? Relating ungulate seasonal movements to tiger spatial organization in the Russian Far East

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Abstract

Wild, solitary felids demonstrate a variety of spacing patterns, with diversity in spatial organization largely attributed to variations in abundance and distribution of important resources, particularly prey. We examined the relationship between territoriality of female Amur tigers *Panthera tigris altaica* and seasonal movements of a key prey species, Manchurian red deer *Cervus canadensis xanthopygus*, in the Russian Far East. We predicted that despite considerable seasonal fluctuations in productivity, red deer density does not change seasonally within tigress home ranges. We analyzed radio-telemetry data to identify directional movements of deer as an indicator of relative changes in seasonal red deer abundance and distribution, and we looked for seasonal shifts in home ranges of tigresses that could signify tracking of migratory prey. We failed to detect either seasonal shifts in tigress home ranges or significant differences in seasonal prey abundance. Most red deer were sedentary, while those that migrated demonstrated varying directionality of movements. Relatively low average snow depth likely reduced directional migratory tendencies in prey populations. Despite existing theory that might predict high overlap of Amur tiger home ranges, our results suggest that exclusive spacing patterns in this tiger subspecies are at least partly explained by the absence of major spatial and temporal changes in ungulate abundance and distribution. We submit that the assumption that home-range overlap should increase with increasing home-range size may require further evaluation in cases such as that of Amur tigers.

Introduction

Spacing patterns of wild, solitary felids vary both intra- and interspecifically, in terms of both home-range size and overlap between individuals (Macdonald, Mosser & Gittleman, 2010). Abundance and distribution of key food resources are proposed to be the primary factors regulating felid spatial organization, particularly for females (Seidensticker *et al.*, 1973; Sandell, 1989; Macdonald *et al.*, 2010). Sandell (1989) argued that home ranges of solitary female carnivores should be just large enough to contain sufficient prey for reproduction, and several studies have demonstrated a direct, inverse relationship between prey biomass and felid home-range size (Ward & Krebs, 1985; Litvatitis, Sherburne & Bissonette, 1986; Karanth *et al.*, 2004). Home-range size, in turn, should influence overlap, with defense of exclusive territories becoming more difficult with increasing territory size (Jetz *et al.*, 2004). Moreover, exclusivity of home ranges is expected only when food resources are evenly distributed both spatially and tem-

porally (Sandell, 1989). If prey resources vary in space or time, the home range must be large enough to support an animal during periods of lowest prey abundance, but may otherwise contain a surplus of food resources, allowing several animals to utilize the same area.

The tiger *Panthera tigris* occurs from the tropical forests of south Asia to the temperate forests of the Russian Far East, with variations in prey composition and availability throughout its geographic range (Sunquist, Karanth & Sunquist, 1999; Miquelle *et al.*, 2010). Consequently, we may expect variation in tiger spacing patterns, as has been documented for other widely distributed felids such as cougars *Puma concolor*, leopards *Panthera pardus* and cheetahs *Acinonyx jubatus* (Stander *et al.*, 1997; Logan & Sweaner, 2001; MacDonald *et al.*, 2010). Yet, data on tigers are scarce. In Chitwan National Park, Nepal, tiger prey were highly abundant, fairly evenly distributed and demonstrated no large-scale shifts in annual distribution (Tamang, 1982). Accordingly, tigresses retained small (20 km²), exclusive home ranges (Smith, McDougal &

Sunquist, 1987). In the mountainous Amur tiger (*P.t. altaica*) habitat of the Russian Far East, prey densities are low (Miquelle *et al.*, 2010), and, as a result, Amur tigress home ranges are among the largest reported for any felid (384 km²; Goodrich *et al.*, 2010). Prey distribution patterns are poorly documented, but it is commonly held that ungulate densities vary both spatially and temporally due to seasonal environmental fluctuations, which are known to induce ungulate migrations in other mountainous northern systems (Adams, 1982; Luccarini *et al.*, 1997). Thus, limited productivity and a strongly seasonal environment appear to provide a sound basis for predicting non-exclusive spacing patterns at the northern extreme of tiger range.

However, several early studies found that overlap of Amur tigress home ranges is negligible (Abramov, 1962; Matyushkin, Zhivotchenko & Smirnov, 1980; Yudakov & Nikolaev, 1987), and recent research using radio-telemetry (Goodrich *et al.*, 2010) has corroborated these conclusions, suggesting the need to re-examine predictions about seasonal variability of ungulate distributions in the Russian Far East. If, contrary to expectations, year-round densities of key tiger prey species are stable, then such stability could provide one mechanism for the existence of large, yet exclusive home ranges in Amur tigresses.

Therefore, we sought to assess seasonal densities of the most important prey species in central and northern Russian tiger range, Manchurian red deer *Cervus canadensis xanthopygus* (Miquelle *et al.*, 2010). Because snow track surveys traditionally conducted in Russia (Stephens *et al.*, 2005) do not allow comparable estimates of ungulate numbers in summer, and thick vegetative cover precludes summer-season line transect sampling and aerial surveys, we analyzed movements of radio-collared red deer as an alternative to directly measuring red deer abundance in multiple seasons. We evaluated distribution of red deer telemetry locations in relation to tigress home ranges, assuming that if a large number of deer moved into or out of a tigress home range in any given season, it would be representative of a change in the relative abundance of prey available to the tiger. We predicted that prey densities do not change seasonally within Amur tigress home ranges, and that therefore either (1) seasonal movements of red deer do not occur, or occur at low frequencies; (2) seasonal movements of red deer occur, but movements are concentrated within a single tigress home range (i.e. overall prey density within the tigress home range does not change); or (3) there is equal movement of red deer both into and out of individual tigresses' home ranges.

Materials and methods

Our study area comprised the south-eastern portion of the 390 184 ha Sikhote-Alin Biosphere Reserve and adjacent territories, Primorsky Krai, Russian Far East (44°46'N, 135°48'E) (Fig. 1). The Reserve is dominated by the Sikhote-Alin Mountains (most peaks below 1000 m), with winter tiger and ungulate habitat extending from the coast to elevations of approximately 800 m. All study animals inhabited the area bordered by the Sea of Japan to the east and the Khuntami

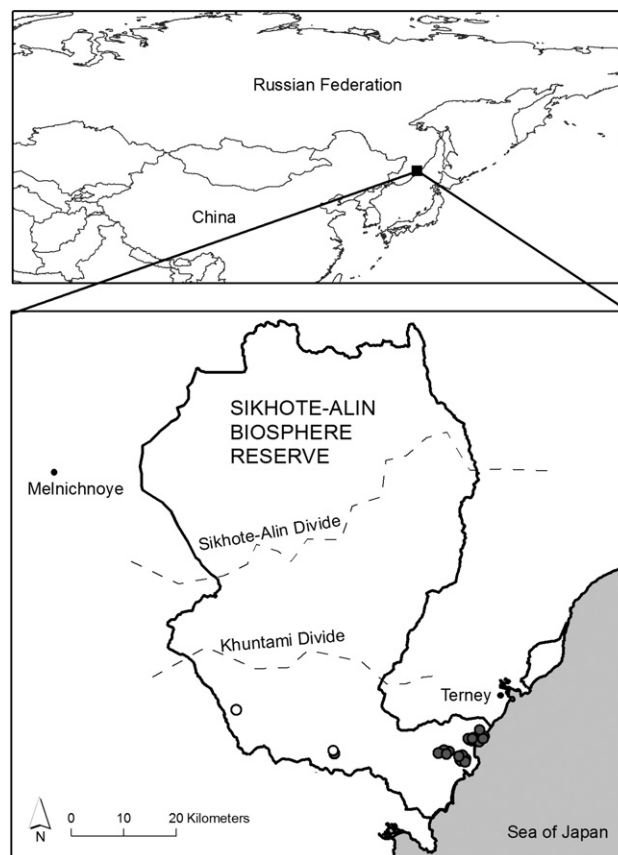


Figure 1 Study area and capture locations of red deer *Cervus canadensis xanthopygus* in Sikhote-Alin Biosphere Reserve, Russian Far East. Locations of deer captured in summer are denoted by open circles. Winter capture locations are denoted by gray circles.

Divide to the west (Fig. 1). The most common forest types were oak *Quercus mongolica* and Korean pine *Pinus koraiensis*-broadleaved forests, and climate was characterized by relatively dry, cold winters and moderately hot, wet summers. Winters were warmer along the coast (−14°C, January) with lower snow depths (averaging 11.7 cm in the last third week of January) than inland (−24°C, 21.0 cm) (Terney and Melnichnoye weather station data, 1940–1999).

Telemetry data were obtained for 29 red deer from December 1998 to May 2002. Deer were captured in baited corral and box traps in winter mostly along the coast (Fig. 1) and fitted with standard very high frequency radio-collars (Telonics, Inc., Mesa, AZ, USA). Locations were obtained five to seven times per week using triangulation from points reached by foot or automobile. Aerial locations of migrating deer were occasionally taken from an Antonov-2 biplane.

Tiger telemetry data were obtained year-round on foot, from vehicles and by air for resident adult tigresses from 1992 to 2008; nearly all resident female tigers inhabiting the study area were monitored during this period (Goodrich *et al.*, 2001, 2010). All tigress home ranges were adjacent to one another.

Home ranges of six tigresses spatially overlapped locations of red deer, but only three tigresses temporally overlapped radio-collared deer (1998–2002). Therefore, we conducted one set of analyses including only the three temporally coincident tigresses, but we also performed a second, separate set of analyses for all six spatially coincident tigresses together. For this second set of analyses, we make three assumptions. (1) Movements of radio-collared deer from 1998 to 2002 were largely representative of red deer movements over the period from 1992 to 2008, particularly as winter weather conditions were not highly variable within this time window (Terney and Melnichnoye weather station data). (2) Red deer movements were unlikely to be influenced by individual tigers or changes in tiger density that occurred outside of the years during which deer were radio-tracked, as tiger densities were relatively high and constant throughout the study area and adjacent regions from 1992 to 2008 (Goodrich *et al.*, 2010), so that no matter where red deer moved, the probability of encountering tigers was similar. (3) If seasonal movements of prey are applied to the full spectrum of tigress home-range configurations recorded in this area, the strength of our conclusions should be stronger.

We calculated summer- and winter-season home ranges (95% contours) for red deer and annual, summer- and winter-season home ranges (95% contours) for tigresses in ArcGIS 9.3.1 using Home Range Tools (Rodgers *et al.*, 2005) and the adaptive kernel method (as recommended by Animal Space Use, Horne & Garton, 2009). Smoothing parameters were calculated using likelihood cross-validation (Horne & Garton, 2006). Telemetry data were divided into summer (10 June–30 September) and winter (1 December–20 April) seasons as defined *post hoc* by timing of ungulate movements; location data collected during the migration period were excluded from seasonal home-range calculations, but not from calculations of annual tigress home ranges. To identify the asymptotic minimum number of locations needed to estimate home-range size, we plotted the number of locations (chosen randomly with respect to date) against home-range size for each species separately. We analyzed only locations separated by at least 24 h, but tests of independence indicated that our data were nevertheless auto-correlated (Schoener, 1981; Swihart & Slade, 1986). We chose not to exclude additional locations because auto-correlated data can contain important biological information and do not reduce accuracy of kernel density home-range estimators (DeSolla, Bonduriansky & Brooks, 1999).

We tested for seasonal shifts in tigress home-range size and location that might indicate tigresses follow migratory movements of prey, as has been documented for other felids (Seidensticker *et al.*, 1973; Crawshaw & Quigley, 1991; Pierce *et al.*, 1999). Percent overlap of each tigress' winter and summer home range was calculated by dividing the area of overlap by the area of the smaller of the two seasonal home ranges (Pierce *et al.*, 1999). For each tigress, we also calculated a yearly fidelity index for sequential, year-long home ranges and a seasonal fidelity index for winter and summer home ranges (averaged for each season for all years) (Logan & Swenor, 2001). Yearly fidelity to home ranges is high

(Goodrich *et al.*, 2010), so we compared the seasonal and yearly fidelity indices, assuming that similar results would indicate an absence of seasonal changes in tigress home-range location.

To determine migratory status of red deer, we measured distances between the geometric centers of summer and winter home ranges, defining migratory deer as those demonstrating no overlap in summer and winter range. To identify predominant patterns of directional movements by migratory deer, we conducted a binomial test (Conover, 1980) using each fall migration event as the sampling unit. We hypothesized that decreasing snow depth near the coast influences directionality of movements, and therefore greater numbers of deer should demonstrate movements to the coast from inland summer ranges than any other movement patterns (e.g. from the coast inland, or between inland home ranges).

To estimate relative seasonal prey availability within tigress home ranges, we calculated proportional overlap of red deer seasonal home ranges and tigress home ranges in summer and winter periods using Hawth's tools for ArcGIS (Beyer, 2004). This approach excluded red deer for which there were insufficient locations to estimate either a winter or a summer home range. To increase sample sizes, we also calculated proportion of seasonal telemetry location points of each deer contained within a tigress home range, assuming proportion of location points contained within a tigress home range provides a reasonable estimate of proportion of time spent within the given home range. Only those deer that survived at least one summer and one winter season were included in our analysis. For one red deer that migrated in 1 year but not another, we treated each year as an independent sample. For a second deer that migrated away from her summer home range for only 2 months each winter, overlap was weighed by the proportion of time she was present in a tigress' home range. Several tigresses permanently relocated to a new home range following death of neighboring females or when allocating a portion of their home range to offspring (Goodrich *et al.*, 2010); because these shifts were permanent (as opposed to potential seasonal or otherwise temporary movements), we treated the two tiger home ranges as separate, independent samples in the overlap analysis.

Due to small sample sizes, we conducted a randomization test (Manly, 2007) to compare the proportion of red deer home ranges (or location points) contained within a tigress' home range in summer to the proportion contained in winter, testing whether the seasonal difference was significantly different from zero. We conducted randomization tests for each tigress home range individually, the group of three tigresses with which red deer were temporally coincident, and all tigress home ranges within the study area together. For each tigress home range, we used 1000 randomizations to construct a distribution for the test statistic and conducted a two-tailed test with a significance level of 5%. During each randomization, the proportion of overlap values was randomly allocated to the summer or winter season. For randomization tests for groupings of tigress home ranges (i.e. for the three tigresses contemporary with collared red deer and for all tigress home ranges together), randomization data from individual tigress

home ranges were combined rather than randomizing across tigress home ranges, thus maintaining the original structure of the dataset.

Results

From 337 to 1747 locations were obtained per tigress (4096 total locations), depending on accessibility and duration monitored. Home-range asymptotes were reached by 44 ± 9 locations. Four of the six tigresses permanently shifted their home ranges once (due to death of neighboring females or division of home range with offspring), resulting in calculation of 10 distinct annual tigress home ranges. Three of these 10 home ranges ($n = 3$ tigresses) were temporally coincident with the period (1998–2002) when ungulate data were collected. Average annual tigress home-range size was $369 \pm 133 \text{ km}^2$ ($n = 10$ home ranges for six tigresses).

There was no significant difference between tigress home-range size in summer and winter ($t = 0.3859$, $n = 9$, $p = 0.71$), and mean overlap between summer and winter home ranges was $86.3 \pm 10.8\%$. The seasonal fidelity index ($88.4 \pm 10.1\%$, $n = 9$) was very high (Logan & Sweanor, 2001) and similar to the yearly fidelity index ($91.6 \pm 6.0\%$, $n = 33$), suggesting that tigresses did not demonstrate seasonal changes in home-range size or location.

A total of 7200 red deer locations was obtained. Seven red deer did not live through either a spring or a fall migration period and therefore could not be characterized as migratory or sedentary. Of the remaining 22 red deer, 12 (55%) were sedentary, 8 (36%) were migratory and 2 (9%) demonstrated mixed movement patterns, migrating only in some years or for only part of a season. Sample sizes needed to calculate red deer home ranges reached an asymptote at 46 ± 11 locations. Home ranges of red deer were, on average, more than 20 times smaller than home ranges of tigresses ($n = 38$ seasonal home ranges for 22 deer). Average distance between summer and winter home ranges of migratory deer was $21.6 \pm 10.4 \text{ km}$, and all migratory deer moved between, not within, tigress home ranges. Of 20 fall migratory movements documented, the number of movements to the coast from inland summer home ranges (12) was not greater than expected (binomial test expected value critical region = 10 ± 4.3), suggesting no clear preferential movement toward the coast in winter.

We estimated proportional overlap of annual tigress home ranges with seasonal home ranges of 16 red deer and with seasonal location points of 19 red deer. Results of randomization tests using overlap of tigress and red deer home ranges were not significant for any individual tigress or for either grouping of tigresses (the three temporally coincident tigresses or all 10 tigress home ranges in the study area from all periods; Fig. 2), suggesting no change in seasonal prey availability. Randomization tests using overlap of tigress home ranges and red deer seasonal location points indicated significant differences between summer and winter prey densities in only one of the 10 individual tigress home ranges and no significant difference for either grouping of tigresses, again suggesting no change in the relative seasonal abundance of prey (Fig. 2).

Discussion

Our results provide at least partial explanation of how Amur tigers are able to retain exclusive home ranges despite their large home-range size. Significant seasonal shifts in distribution of key Amur tiger prey did not occur within tigress home ranges in our study area, as the majority of red deer monitored were sedentary, while migratory individuals collectively demonstrated non-directional movement patterns. Because red deer home ranges were very small in comparison to tigress home ranges, most deer likely remained within one tigress home range not only throughout the year but also throughout their lifetime. While migratory red deer moved between, not within, tigress home ranges, some deer moved in opposite directions, in effect cancelling out 'losses' with 'gains' of prey within a given tigress' home range. Other individuals demonstrated seasonal movements only in some years or spent only part of a winter or a summer on a different range.

Snow depth and condition are considered key factors ultimately driving migratory behavior (Mysterud, Bjornsen & Ostbye, 1997; Ball, Nordengren & Wallin, 2001), with variability in snow depth resulting in mixed migratory patterns (Sabine *et al.*, 2002). In our study area, average January snow depth, even further inland, is not great enough to significantly increase energetic expenditures for movement of red deer (Parker, Robbins & Hanley, 1984; Sweeney & Sweeney, 1984) and is therefore unlikely to induce large-scale migrations.

Most red deer in our sample were captured near the Sea of Japan in winter; thus, we hypothesized, increasing the probability of capturing deer that migrated to milder coastal areas in winter and that would move inland to higher elevations in summer. The bias in capture locations reduced the chances of collaring deer that moved in the opposite direction. Nonetheless, we failed to detect significant differences in the number of deer migrating to or away from the coast or in overall overlap of prey and tigress home ranges in summer versus winter, providing even stronger evidence that red deer seasonal movements were insufficient to significantly change prey densities.

Wild boar were the second most important prey resource in our study area, comprising 28% of tiger kills (Miquelle *et al.*, 2010). We attempted to monitor wild boar, but boar numbers were extremely low during the study period, and our capture success was also low. While small sample sizes prevented formal analyses, movements of those boar tracked in our study area between 1998 and 2002 were largely contained within one tigress home range, with no detectable seasonal or long-distance movement patterns, again suggesting no change in seasonal prey abundance. Secondary prey species in our study area included sika deer, which are highly sedentary (Bromley & Kucherenco, 1983; Danilkin, 1999), and roe deer, which are a very minor part of tiger diets (Miquelle *et al.*, 1996). Therefore, their omission from our analysis is unlikely to have influenced results.

Tigers in our study area exploited a system where a stable, dispersed population of red deer was the primary prey, but variability in ecological conditions could lead to different spacing patterns than those we have documented. There exist historical reports of 'migrating' Amur tigers (Heptner &

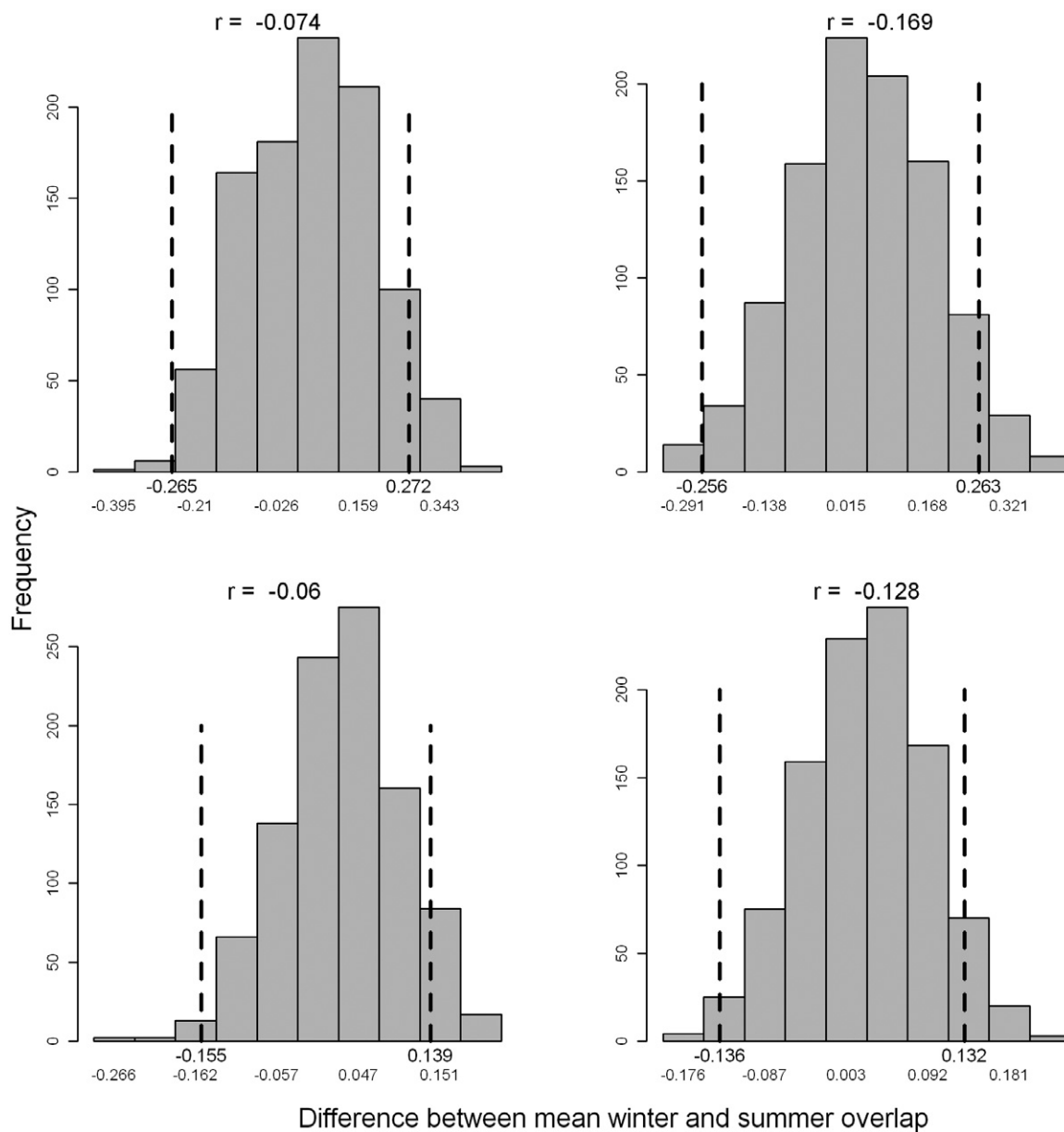


Figure 2 Results of randomization tests for temporally coincident tigris home ranges (top row) and all tigris home ranges (bottom row). Results using proportional overlap of ungulate seasonal home ranges are shown on the left; results using proportional overlap of ungulate seasonal location points are shown on the right. Actual proportion of overlap = r . Each histogram shows the distribution of the 1000 values generated by randomization; dashed lines on the left and right tail of each distribution indicate the value corresponding to the 2.5th and 97.5th quantile of the randomized values. Values of proportional overlap smaller or larger than these quantiles would be deemed statistically significant at the 5% level.

Sludskii, 1992), and often such reports link movements of tigers to large-scale movements of wild boar (Rukovsky, 1963), which were also tigers' primary prey in the early 20th century (Bromley & Kucherenko, 1983). Moreover, snow depth varies greatly in Amur tiger range, and deeper snows could induce more red deer to migrate as well. Thus, it is possible that information from systems with differing prey and weather conditions could reveal flexibility in tiger spatial organization, as has been found for other carnivore species.

While our results support the hypothesis that stable prey densities allow female Amur tigers to retain exclusive home ranges, the existence of territoriality in Amur tigers contradicts theoretical analyses that suggest overlap of large home ranges should be extensive (Jetz *et al.*, 2004) and is incongruent with field studies of other felids, such as leopards and lynx, which demonstrated increasing home-range overlap with increasing home-range size (Schmidt, Jedrzejewski & Okarma, 1997; Stander *et al.*, 1997; Marker & Dickman, 2005). Models

predicting optimal territory size generally assume that defense costs increase directly with home-range size (Hixon, 1980; Schoener, 1983; Jetz *et al.*, 2004); however, individuals with large, exclusive home ranges may adopt strategies to minimize the cost of defense. For instance, scent-marking by tigers (Smith, McDougal & Miquelle, 1989; Protas *et al.*, 2010) clearly conveys information to individuals co-habiting space, potentially reducing the chance of intrusion by neighbors. Therefore, for species like tigers, which are capable of maintaining very large, yet non-overlapping home ranges, fruitful future research may consider identifying mechanisms designed to reduce costs of defense and examining the relationship of territoriality both to these mechanisms as well as to prey availability.

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References

- Abramov, V.K. (1962). On the biology of the Amur tiger, *Panthera tigris longipilis* Fitzinger, 1868. *Vestn. Acta Zool. Soc. Bohemoslovenicae* **26**, 189–202. (in Russian).
- Adams, A.W. (1982). Migration. In *Elk of North America: ecology and management*: 301–321. Thomas, J.W. & Toweill, D.E. (Eds). Harrisburg: Stackpole Books.
- Ball, J.P., Nordengren, C. & Wallin, K. (2001). Partial migration by large ungulates: characteristics of seasonal moose ranges in northern Sweden. *Wildl. Biol.* **7**, 39–47.
- Beyer, H.L. (2004). Hawth's analysis tools for ArcGIS. Available at <http://www.spatialecology.com/htools>.
- Bromley, G.F. & Kucherenko, S.P. (1983). *Ungulates of the southern Far East USSR*. Moscow: Nauka. (in Russian).
- Conover, W.J. (1980). *Practical nonparametric statistics*. New York: John Wiley & Sons.
- Crawshaw, P.G. & Quigley, H.B. (1991). Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *J. Zool. (Lond.)* **223**, 357–370.
- Danilkin, A.A. (1999). *Cervidae*. Moscow: GEOS. (in Russian).
- DeSolla, S.R., Bonduriansky, R. & Brooks, R. (1999). Eliminating autocorrelation reduced biological relevance of home range estimates. *J. Anim. Ecol.* **68**, 221–234.
- Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Kerley, L.L., Quigley, H.B. & Hornocker, M.G. (2010). Social Structure of Amur (Siberian) tigers (*Panthera tigris altaica*) on Sikhote-Alin Biosphere Zapovednik, Russia. *J. Mammal* **91**, 737–748.
- Goodrich, J.M., Kerley, L.L., Schleyer, B.O., Miquelle, D.G., Quigley, K.S., Smirnov, Ye.N., Nikolaev, I.G., Quigley, H.B. & Hornocker, M.G. (2001). Capture and chemical anesthesia of Amur tigers. *Wildl. Soc. Bull.* **29**, 533–542.
- Heptner, V.G. & Sludskii, A.A. (1992). *Mammals of the Soviet Union, Volume II, Part 2: Carnivora*. New Delhi: Amerind Publishing Co.
- Hixon, M.A. (1980). Food production and competitor density as the determinants of feeding territory size. *Am. Nat.* **115**, 510–530.
- Horne, J.S. & Garton, E.O. (2006). Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home range analysis. *J. Wildl. Mgmt.* **70**, 641–648.
- Horne, J.S. & Garton, E.O. (2009). Animal Space Use 1.3. Available at http://www.cnr.uidaho.edu/population_ecology/animal_space_use.htm.
- Jetz, W., Cabone, C., Fulford, J. & Brown, J. (2004). The scaling of animal space use. *Science* **306**, 266–268.
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. & Hines, J.E. (2004). Tigers and their prey: predicting carnivore densities from prey abundance. *Proc. Natl. Acad. Sci. USA* **101**, 4854–4858.
- Litvatis, J.A., Sherburne, J.A. & Bissonette, J.A. (1986). Bobcat habitat use and home range size in relation to prey density. *J. Wildl. Mgmt.* **50**, 110–117.
- Logan, K.A. & Sweanor, L.A. (2001). *Desert puma: evolutionary ecology and conservation of an enduring carnivore*. Washington, DC: Island Press.
- Luccarini, S., Maraso, D., Lanelle, G., Valotie, M., Mauri, L. & Apollonio, M. (1997). Home range patterns of red deer *Cervus elaphus* in the Eastern Italian Alps. In *2nd World Conference on Mountain Ungulates, Abstract Volume*: 93. Aosta, Italy: Saint-Vincent.
- Macdonald, D.W., Mosser, A. & Gittleman, J.L. (2010). Felid society. In *Biology and conservation of wild felids*: 125–160. Macdonald, D.W. & Loveridge, A.J. (Eds). Oxford: Oxford University Press.
- Manly, B.F.J. (2007). *Randomization, bootstrap and Monte Carlo methods in biology*. 3rd edn. Boca Raton: Chapman & Hall/CRC.
- Marker, L.L. & Dickman, A.J. (2005). Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *S. Afr. J. Wildl. Res.* **35**, 105–115.

- Matyushkin, E.N., Zhivotchenko, V.I. & Smirnov, E.N. (1980). *The Amur tiger in the USSR*. Gland: IUCN.
- Miquelle, D.G., Smirnov, E.N., Quigley, H.G., Hornocker, M., Nikolaev, I.G. & Matyushkin, E.N. (1996). Food habits of Amur tigers in Sikhote-Alin Zapovednik and the Russian Far East, and implications for conservation. *J. Wildl. Res.* **1**, 138–147.
- Miquelle, D.G., Goodrich, J.M., Smirnov, E.N., Stephens, P.A., Zaumyslova, O.Yu., Chapron, A., Kerley, L., Murzin, A.A., Hornocker, M.G. & Quigley, H.B. (2010). The Amur tiger: a case study of living on the edge. In *The biology and conservation of wild felids*: 325–339. Loveridge, A.J. & MacDonald, D.W. (Eds). Oxford: Oxford University Press.
- Mysterud, A., Bjornsen, B.H. & Ostbye, E. (1997). Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway. *Wildl. Biol.* **3**, 27–33.
- Parker, K.L., Robbins, C.T. & Hanley, T.A. (1984). Energy expenditures for locomotion by mule deer and elk. *J. Wildl. Mgmt.* **48**, 474–489.
- Pierce, B.M., Bleich, C., Wehausen, J.D. & Bowyer, T. (1999). Migratory patterns of mountain lions: implications for social regulation and conservation. *J. Mammal* **80**, 986–992.
- Protas, Y.L., Seryodkin, I.V., Nisen, S., Goodrich, J.M., Smirnov, E.N. & Miquelle, D.G. (2010). Characteristics of marking activity of the Amur tiger. In *The Amur tiger in Northeast Asia: planning for the 21st century*: 135–138. Zhuravlev, Y.N. (Ed.). Vladivostok: DalNauka.
- Rodgers, A.R., Carr, A.P., Smith, L. & Kie, J.G. (2005). *HRT: home range tools for arcgis*. Thunder Bay: Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research.
- Rukovsky, N.N. (1963). The effect of periodicity of the yield of pine nuts on mammals in the Eastern Sikhote-Alin. *Zool. Zhurnal* **42**, 1741–1742. (in Russian).
- Sabine, D.L., Morrison, S.F., Heather, A.W., Ballard, W.B., Forbes, G.J. & Bowman, J. (2002). Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick. *J. Wildl. Mgmt.* **66**, 718–728.
- Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behavior, ecology, and evolution*: 164–182. Gittleman, J.L. (Ed.). New York: Comstock Publishing Associates.
- Schmidt, K., Jedrzejewski, W. & Okarma, H. (1997). Spatial organization and social relations in the Eurasian lynx population in Bialowieza Primeval Forest, Poland. *Acta Theriol. (Warsz.)* **42**, 289–312.
- Schoener, T.W. (1981). An empirically based estimate of home range. *Theoret. Pop. Biol.* **20**, 281–325.
- Schoener, T.W. (1983). Simple models of optimal feeding-territory size: a reconciliation. *Am. Nat.* **212**, 608–629.
- Seidensticker, J.C. IV, Hornocker, M.G., Wiles, W.V. & Messick, J.P. (1973). Mountain lion social organization in the Idaho Primitive Area. *Wildl. Monogr.* **35**, 3–60.
- Smith, J.D.L., McDougal, C. & Miquelle, D.G. (1989). Scent marking in free-ranging tigers, *Panthera tigris*. *Anim. Behav.* **37**, 1–10.
- Smith, J.L., McDougal, C.W. & Sunquist, M.E. (1987). Female land tenure system in tigers. In *Tigers of the world: the biology, biopolitics, management, and conservation of an endangered species*: 97–109. Tilson, R.L. & Seal, U.S. (Eds). Park Ridge: Noyes Publication.
- Stander, P., Haden, P.J., Kagece, I. & Ghau, I. (1997). The ecology of asociality in Namibian leopards. *J. Zool. (Lond.)* **242**, 343–364.
- Stephens, P.A., Zaumyslova, O.Y., Miquelle, D.G. & Hayward, G.D. (2005). Temporal analyses of ungulate population dynamics in Sikhote-Alin Zapovednik. In *Tigers of Sikhote-Alin Zapovednik ecology and conservation*: 89–96. Miquelle, D.G., Smirnov, E.N. & Goodrich, J.M. (Eds). Vladivostok: PSP. (in Russian).
- Sunquist, M.E., Karanth, K.U. & Sunquist, F. (1999). Ecology, behavior, and resilience of the tiger and its conservation needs. In *Riding the Tiger: meeting the needs of people and wildlife in Asia*: 5–18. Seidensticker, J., Christie, S. & Jackson, P. (Eds). Cambridge: Cambridge University Press.
- Sweeney, J.M. & Sweeney, J.R. (1984). Snow depths influencing winter movements of elk. *J. Mammal* **65**, 524–526.
- Swihart, R.K. & Slade, N.A. (1986). The importance of statistical power when testing for independence in animal movements. *Ecology* **67**, 255–258.
- Tamang, K.M. (1982). *The status of the tiger (Panthera tigris) and its impact on principal prey populations in Royal Chitwan National Park, Nepal*. PhD dissertation, Michigan State University.
- Ward, R.M.P. & Krebs, C.J. (1985). Behavioural responses of lynx to declining snowshoe hare abundance. *Can. J. Zool.* **63**, 2817–2824.
- Yudakov, A.G. & Nikolaev, I.G. (1987). *Ecology of the Amur tiger: winter long-term observations in the western part of the middle Sikhote-Alin, 1970–1973*. Moscow: Nauka. (in Russian).