ORIGINAL PAPER

The influence of reproductive status on home range size and spatial dynamics of female Amur tigers

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Abstract

In populations of wild felids, social status is one of the most important factors shaping home range size and spacing patterns. For female Amur tigers (*Panthera tigris altaica*), we documented significant changes to the structure of home ranges and core areas during cub-rearing. We used VHF telemetry data collected over 18 years in Sikhote-Alin Biosphere Reserve, Russia, to assess the following: (1) home range and core area size and (2) spatial shifts with and without cubs and (3) spatial shifts associated with philopatry. Home range and core area sizes of females collapsed by 60% after birthing, with recovery requiring 18 months. We hypothesized that usurpation of temporarily abandoned territory by other females during cub-rearing was a possibility, but aside from philopatry, we did not observe a loss of territory or evidence of competition for space. Home range boundaries changed little during cub-rearing but shifting core areas revealed that females were using different segments of their home range while rearing cubs, contradicting the notion of a single, most important core area for breeding females. Our results support two hypotheses of space use by large carnivores: that adult breeding females achieve higher reproductive success by maintaining a home range just big enough to feed herself and her offspring, and a second hypothesis that females expand home range size when space is available to allocate land to daughters. We suggest that these hypotheses are not mutually exclusive, but explain patterns of space use by female felids under different demographic conditions.

Keywords Core area · Cub-rearing · Female Amur tigers · Home range size · Proportional overlap · Spatial change

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Introduction

Large carnivore population densities are mostly determined by prey availability (Carbone and Gittleman 2002; Hayward et al. 2007), but given the variation in sex-specific strategies to maximize reproductive success, it is predicted that male and female spacing patterns will respond differently to varying prey densities. Sandell (1989) proposed that space-use patterns of female felids follow a foraging optimality rule of area minimization, with higher reproductive success achieved by maintaining a home range just big enough to feed a female and her offspring during the most critical period of the year. However, an alternative hypothesis suggests that home range size of females may expand beyond the minimum when a carnivore population is not at carrying capacity, or when space is available, allowing females the opportunity to allocate space to female offspring who can benefit from local knowledge of resources, thereby increasing overall fitness (Fattebert et al. 2016).

Before such philopatry can occur, however, females must successfully raise young to the stage where they are ready to

disperse, or inherit a portion or all of their mother's home range. The process of caring for young has been demonstrated to dramatically influence space use by female felids (Hemker et al. 1984; Maehr et al. 1989; Bailey 1993; Schmidt 1998; Odden and Wegge 2005; Criffield et al. 2018). Generally, these studies have demonstrated that home range size of felid mothers greatly contracts with the birth of a new litter and stays small while cubs/kittens are kept at a den site. As young become more mobile, dens are generally abandoned, the young travel with their mother, and home range use expands (Maehr et al. 1989; Schmidt 1998).

Dramatic reductions in home range size for any extended period could allow other females to usurp an abandoned portion of a territory, as happens with the death or disappearance of resident females (Smith et al. 1987; Goodrich et al. 2010). Fights over territorial boundaries, although rare, do occur and can result in injuries (Smith et al. 1987). This risk has rarely been considered an issue with the birthing process for felid species (Petrunenko et al. 2019), but the contracted area used while rearing young represents a potential opportunity for other females competing for space. The level of risk likely increases as the length of time that females are absent from some portion of their home range increases. Such potential loss of territory consequently threatens a female's ability to increase fitness via natal philopatry. Hence, if the reduction in home range size is essential during the early stages of cub-rearing, it would be expected that mothers attempt to quickly reassert their presence across their entire home range to avoid potential confrontation or loss of territory. For most felid species, little is known about the rate and pattern of female home range contraction and expansion associated with cub-rearing, or when/if full recovery of home ranges occurs.

Studies in the Russian Far East have shown that female Amur tigers (*Panthera tigris altaica*) maintain the largest home ranges known for this species anywhere across its range (Goodrich et al. 2010; Hojnowski et al. 2012; Hernandez-Blanco et al. 2015). Female tigers demonstrate territoriality, with relatively little overlap in home ranges (Goodrich et al. 2010; Simcharoen et al. 2014; Hernandez-Blanco et al. 2015), suggesting that they must patrol, mark, and defend their home ranges (Smith et al. 1987). Seasonal shifts in home range usage have not been detected for tigresses (Hojnowski et al. 2012; Simcharoen et al. 2014), but, as with other felids, multiple studies have documented that home range size of tigresses greatly contracts after the birth of cubs (Goodrich et al. 2010; Majumder et al. 2012; Petrunenko et al. 2019). This collapse of home range size appears to be associated with the immobility of young cubs, nursing requirements, and the need to protect cubs from predation during their most vulnerable period (Maehr et al. 1989; Beier et al. 1995; Odden and Wegge 2005; Petrunenko et al. 2019).

Less attention has been paid to how home range contraction, associated with philopatry and/or cub-rearing, may

influence the configuration of a female's core area. Presumably, availability of prey should be one of the key parameters defining core areas for female carnivores (Petrunenko et al. 2016) but after birthing, location of a secure den site that reduces chances of predation on young may be temporarily more important to felid mothers than prey density (Beier et al. 1995; Schmidt 1998). If such is the case, we would expect that core areas might shift dramatically during the early stages of cub-rearing, but gradually return to the original core area as cubs mature and eventually disperse.

Previous studies on Amur tigers indicate that while boundaries of home ranges can sometimes change, core areas, generally presumed to represent the most important portion of an individual's home range, remain stable over time (Hernandez-Blanco et al. 2015), unless the animal completely changes home range location. However, if females allocate a portion of their core areas to female offspring, core area configuration could be altered. For tigers, it is not clear if females allocate a portion of their core area to their daughters, or retain that core area while sacrificing other parts of their territory.

We assessed how the cub-rearing process influences home ranges and core areas of Amur tigresses, looked for evidence of incursion by other females during cub-rearing, and considered how philopatry influences the structure of a female's home range and core area. First, we assessed how reproductive status and age of cubs influence the size of core areas and total home range areas. We assessed how quickly home ranges contract with birthing, how quickly females reassert their presence across home ranges, and how closely pre-birth home range and core area boundaries match those re-established after cub dispersal. We assessed whether a decrease in size or shifting of home range boundaries of females might be evidence of incursion by another female, or related to philopatry, and whether an increase in home range size was a precursor to females allocating a portion of their home range to daughters. We assessed how core areas shift in relation to the presence and age of cubs, to what extent core areas during periods of cub-rearing overlap with core areas during periods without cubs, and whether females allocated a portion of core areas to daughters. Understanding these space-use dynamics may help clarify how female felids deal with the multiple constraints associated with rearing young, and the consequences of philopatry on the structure and location of female home ranges.

Methods

Study area

All study animals inhabited the coastal portion of the 4000 km^2 Sikhote-Alin Biosphere Reserve (SABZ) and adjacent

territories in the Russian Far East (Fig. 1). This region is dominated by the Sikhote-Alin Mountain Range with most peaks below 1200 m (Gromyko 2005). The climate of the study area is characterized by strong seasonality with dry, cold winters, warmer along the coast (mean = - 12.9 °C, January), and warm, humid summers (mean = 15 °C). Vegetation communities vary from Mongolian oak (*Quercus mongolica*) forests along the coast to mixed conifer—deciduous forests inland, including Korean pine (*Pinus koraiensis*), larch (*Larix komarovii*), birch (*Betula* spp.), Ajan spruce (*Picea ajanensis*), and Manchurian fir (*Abies nephrolepis*). The preferred prey species of tigers in the study area are red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*), with sika deer (*Cervus nippon*) and roe deer (*Capreolus pygargus*) also common in the diet (Miquelle et al. 2010; Miller et al. 2014).

Data collection

To examine spatial changes in home range and core area associated with cub-rearing, we used telemetry data collected from February 1992 to June 2010 from radio-collared tigresses captured in leg-hold snares or darted from helicopters.

Tigers were anesthetized with ketamine mixed with xylazine or medetomidine (Goodrich et al. 2001), or with Zoletil (Lewis and Goodrich 2009) and fitted with standard very high frequency (VHF) radio-collars (Telonics, Mesa, AZ, USA). We collected over 7000 telemetry locations: (1) from the ground on foot and from vehicles using triangulation (51%); (2) by approaching from 100 to 400 m and partially circling a tiger (9%); and (3) from the air (40%) in an AN-2 biplane, MI-2 helicopter, or MI-8 helicopter. The number of locations per tigress varied largely due to accessibility, collar lifespan, and tigress survival, but averaged 10 times per month with the majority of locations taken during the day from 8 a.m. to 8 p.m. (94%). Research on wild tigers was approved by the Russian Federation's Ministry of Natural Resources, followed the American Society of Mammalogist Guidelines, and was approved by the Wildlife Conservation Society's Animal Care and Use Committee.

We estimated home range characteristics only for females that had been monitored for at least two months prior to birthing and for at least 4 months after giving birth. We estimated age based on body size, tooth eruption, tooth wear and staining, or from known birth dates (cubs of radio-collared
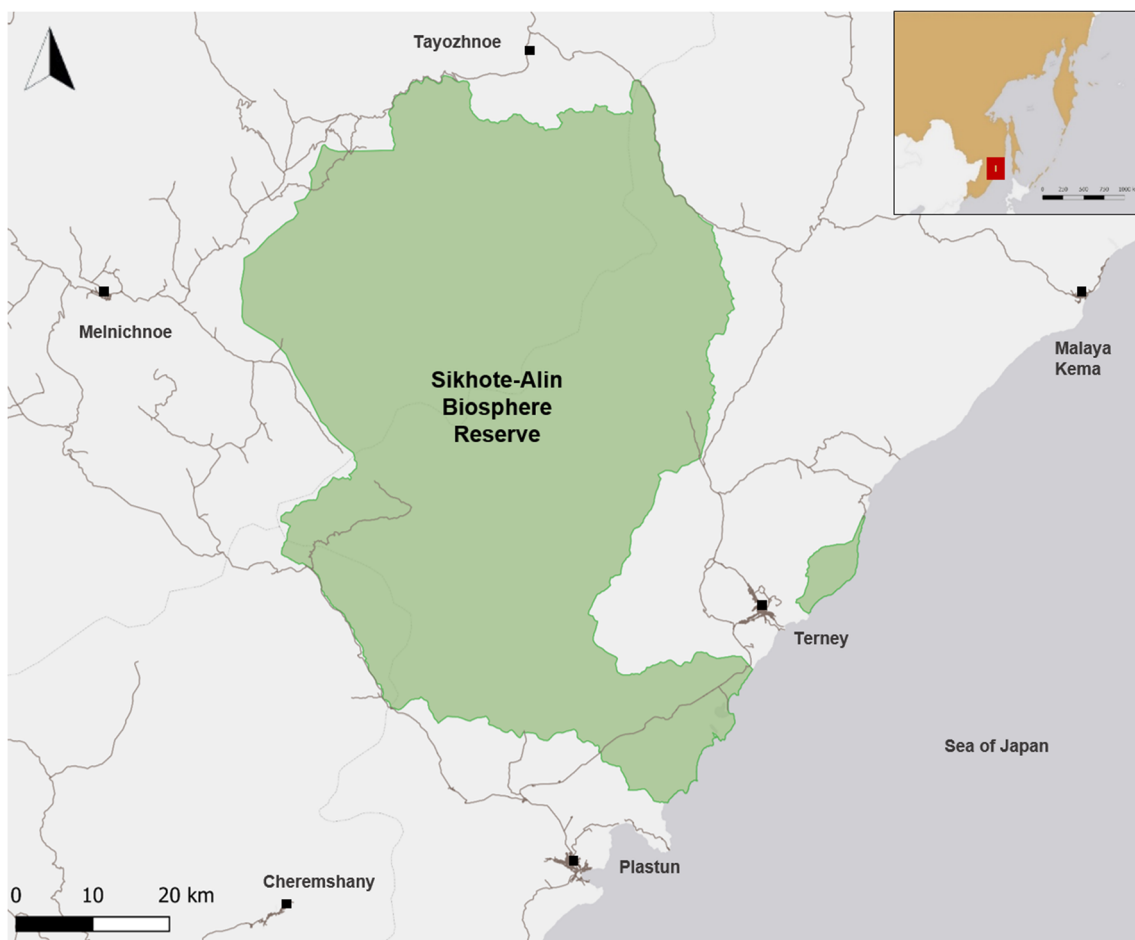

Fig. 1 Radio tracking of collared Amur female tigers was conducted between February 1992 and June 2010 in and around the Sikhote-Alin Biosphere Reserve in the Russian Far East

mothers; Goodrich et al. 2010). Birth dates of cubs were estimated from the first day of an extended localization of a female's movements (average precision was ± 7 days) followed by evidence of cubs (usually tracks) of the appropriate age (size) (Kerley et al. 2003). Birth dates were asynchronous, occurring in all but 2 months of the year (Kerley et al. 2003). The date females were first seen with cubs (to estimate the number of cubs) and last seen with cubs (to estimate loss of cubs or dispersal) was usually based on tracks in snow or mud, and occasionally based on camera trap photographs. Relatedness of individuals was determined based on observations of cubs together and in association with their mothers (Kerley et al. 2003) and unpublished genetic analyses.

Data analysis

We divided data on every tigress into 6 periods: 2 periods without cubs (solitary before and after cub-rearing) and 4 periods of cub-rearing (Table 1). The first solitary period began as soon as we captured a female (if she was without cubs) or when she was estimated to be at least 3 years old and ended with the birth of a litter. The second solitary period began with the 19th month after birthing (unless cubs were lost earlier) because on average, cubs disperse from their natal home range at 18 months (Kerley et al. 2003), and are largely independent of their mothers by that age. The second solitary period ended with the birth of the next litter. We used the entire length of a period a female was without cubs (which was generally longer than periods defined with cubs) because this gave more precise estimates of home range and core area sizes during these solitary periods, and more importantly, using shorter intervals would potentially omit important information about how females used their home range when without cubs. We felt this was more important than maintaining the same time intervals for estimating these parameters. We subdivided the cub-rearing phase into periods which coincided with stages of the cubs' physical and social development (Yachmennikova et al. 2017): 0–4 months—cubs are fully dependent on their

mothers for the first two months, feeding exclusively on milk and staying near the den and then in the second 2 months follow mothers to kill sites and temporary den sites as they begin to eat meat (Petrunenko et al. 2019); 5–8 months—cubs actively explore their home range, deciduous teeth fully emerge, and cubs begin developing hunting skills; 9–12 months—cubs start to hunt separately from their mother, begin exhibiting marking behavior and aggression towards each other; and 13–18 months—cubs become independent, spend more time alone, hunting on their own, but still associate with their mother and litter mates (Table 1).

As our sampling effort was significantly influenced by logistic constraints, weather conditions, and accessibility, we obtained a wide range of locations per period, per tigress, and per litter. No analytical method is available to determine the necessary sample size for nonparametric home range estimators because they do not have an associated variance estimator (White and Garrott 1990; Seaman et al. 1999). Researchers have subsequently tried to define a sufficient number of locations using various methods, including standard linear regression (Barg et al. 2005), calculation of the approximate asymptote associated with home range size and sample size (e.g. Goodrich et al. 2010), visual inspection of the area-observation curve for evidence of an asymptote, and limitations on incremental increases in home range area as sample size increases (Harless et al. 2010). Approximately 20 percent of our home range estimates used less than 20 data points, so we tested for a potential bias of small sample size on home range/core area size estimates using standard linear regression. We calculated home ranges (95% contours) and core areas (50% contours) for each of the six periods associated with each litter using the nonparametric kernel density estimator (KDE) with a plug-in selector (bandwidth matrix), as this data-driven technique provides a good solution for animals moving widely across much of their home ranges, and is appropriate with radiotelemetry errors common in mountainous areas (Gitzen et al. 2006). However, this approach does have a tendency to oversmooth boundaries and overestimate home

Table 1 Home range and core area size of ten Amur tigresses when solitary (before and after a litter) and when with cubs during 4 periods from birth to dispersal, based on 95% and 50% kernel-estimated contours, in and around Sikhote-Alin Biosphere Zapovednik, Russian Far East, 1992–2010

Period	Abbreviation	Number of periods	Average number of locations	Home range size + 95% CI	Core area size + 95% CI
Solitary before cubs	S1	14	92.5 ± 32.1	413.5 ± 77.6	125.4 ± 21.2
Cubs 0–4 months old	C0–4	24	34.3 ± 6.7	177.3 ± 53.5	39.2 ± 13.1
Cubs 5–8 months old	C5–8	17	24.7 ± 7	259.0 ± 63.0	72.1 ± 22.6
Cubs 9–12 months old	C9–12	17	26.5 ± 8.9	300.5 ± 89.2	81.6 ± 25.3
Cubs 13–18 months old	C13–18	15	35.5 ± 11	403.3 ± 105.1	111.6 ± 26.9
Solitary after cubs	S2	15	88.4 ± 38.6	483.8 ± 104.3	128.4 ± 32.0

range size (Gitzen et al. 2006). We performed the analysis using the "ks" package combined with the "adehabitat" package in R statistical software (Chacon and Duong 2018). We calculated smoothing parameters using the plug-in variance matrix H because $h_{plug-in}$ converges for large multimodal datasets and results in reasonable estimates (Chacón and Duong 2010). To reduce bias, for each run, we randomly selected one location per day. We clipped portions of home ranges and core areas extending into the Sea of Japan and then estimated size of the remaining area using QGIS 2.18 (QGIS Development Team 2016).

We used the 50% kernel isopleth as an indicator of core area. Although this approach has been criticized (Seaman and Powell 1990), using this simpler, more direct estimator of core area has been considered by others to be the most appropriate method (Fieberg and Börger 2012) and is commonly used by others for similar purposes (Lendrum et al. 2014; Elbroch et al. 2016; Fattebert et al. 2016). We estimated core areas to understand the dynamics of use within a home range over time by looking for overlap between periods, and found this estimator simple and sufficient to measure these changes.

We looked for variation in three parameters of home ranges/core areas across the periods: (1) home range/core area size; (2) proportional overlap of home ranges/core areas between the first solitary period and all other periods (to determine if there are spatial shifts away for the original home range or core area); and (3) proportional overlap between consecutive periods (to detect time-dependent shifts in home range/core area location during cub-rearing). We looked for significant differences in overlap between pairs of periods to provide an indication that the location of home ranges/core areas had shifted. Percent overlap of pairs of home range and core area estimates was calculated using the formula:

$$Hij = Aij/Ai,$$

where Aij is the area of overlap and Ai the area of solitary period or the second of consecutive periods (Fieberg and Kochanny 2005).

We built three pairs (home range and core area) of generalized linear mixed models (GLMM) to test for the variation in these three parameters in which size, percent overlap with the first solitary period, and percent overlap between consecutive periods were the response variables, period was the independent variable, and litter (each litter of each female) was a random effect. The general form of the model was:

$$\ln(y) = \beta_0 + \beta_1 \text{period}_{ij} + u_j + \varepsilon_{ij},$$

where $\ln(y)$ is the natural log-transformed home range/core area size or proportional overlap between periods, and $u_j \sim N(0, d^2)$ is the intercept of random effect (litter), $\varepsilon_{ij} \sim N(0, d^2)$ (Bolker et al. 2009).

We checked residuals of every model for normality using the Shapiro-Wilk test, and if data were not distributed normally, we applied the Box-Cox transformations for the GLMMs, after which we ran the model again. If the tested p values were significant ($p < 0.05$) in at least one of the periods, we ran simultaneous multiple comparisons (Tukey's post hoc tests) for general linear hypotheses (Hothorn et al. 2019) to identify which periods differed. We conducted all analysis using the R statistical software version 3.5.3 (R Development Core Team 2019).

We identified major reductions in home range size (more than 100 km^2) and then looked for evidence of an incursion by another female (e.g., tracks of a different female in snow or mud, or movements of a radio-collared female), or allocation of a home range (or portion of it) to a daughter of the previous litter. Similarly, we identified home ranges that were 200 km^2 larger than average (average = 390 km^2; Goodrich et al. 2010) and looked for evidence of whether this led to philopatry in the subsequent litter (mostly by tracking radio-collared daughters).

Results

We monitored 10 female tigers both as solitary individuals and in association with 27 litters (with 1 to 6 litters per female—see Online Resource 1, Supplemental Table 1). We tracked tigresses for a minimum of five and maximum of 156 months (70.8 months average). The total number of locations per female ranged from 69 to 1823 (mean 617.8 ± 304.5 locations) with the variation due to remoteness and inaccessibility of the area, duration of the monitoring period, collar lifespan, and tigress survival. The average number of locations per period ranged from nearly 25 to 92 (Table 1). Our results indicated no significant correlation between the number of locations and home range or core area sizes ($p = 0.588$ and $p = 0.830$ respectively); thus, we included all our periods in the analyses. Sample sizes of the cub-rearing periods varied due to cub mortality (60% of newborn kittens survived the first year). We calculated 101 home ranges and core areas (total 202 estimates) for 29 solitary and 72 cub-rearing periods (Table 1).

Home range and core area size

Based on the results of GLMM models, we found significant differences between solitary and cub-rearing periods, in both home range and core area size (Table 1). Home range size did not appear to decline gradually during the solitary period leading up to birthing, but dropped precipitously after birthing. Home range size of females declined by 60% in the first cub-rearing period after giving birth, the core area dropped by 69% (Fig. 2), and both were significantly different from all but the next (5–8 months) cub-rearing period (Fig. 2). After

Fig. 2 Home range and core area size of ten female Amur tigers without cubs (solitary before and after cubs) and during four periods of cub-rearing (notation as "cubs" and months since birth, e.g., "cubs 0–4" for the period from birth to 4 months) for 27 litters, based on 95% and 50% kernel-estimated contours, in and around Sikhote-Alin Biosphere Reserve, Russian Far East, 1992–2010
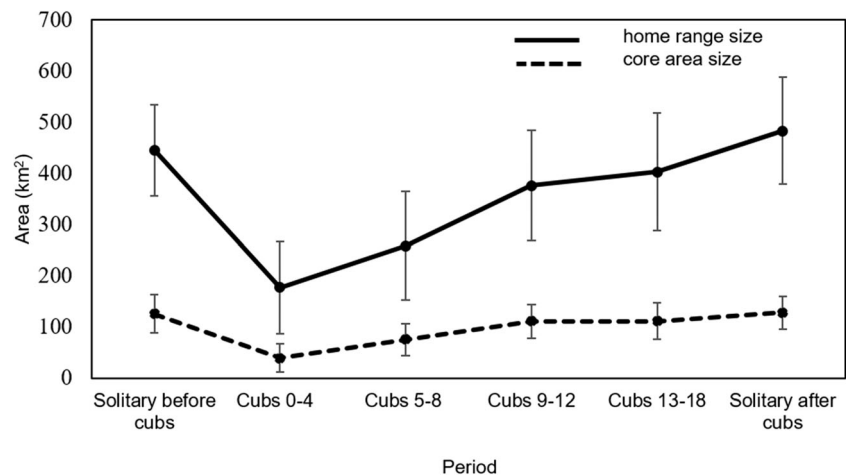
the first 4-month period with cubs, home range size steadily increased by about 20% through each of the subsequent three cub-rearing periods, and even after dispersal of cubs, at which point home ranges were on average larger (but not significantly) than the solitary period before giving birth (Fig. 2). When cubs were 1 year old, home range size was still only 70% of the female's original solitary home range, but the core area was already 97% of its original size (Table 1, Fig. 2). Overall, by the time cubs were dispersing, home range and core area size of females had completely recovered to the area of their initial size prior to cubs. The patterns of decline and recovery in home range and core area size were very similar, though core area size recovered slightly more quickly, and home range size varied more dramatically (Fig. 2).

Spatial shifts

Overlap of areas used while cub-rearing within a female's original home range declined slowly during the cub-rearing process and continued afterward (Fig. 3). We observed significant differences in home range overlap between the early and later stages of cub-rearing (Online Resource 1, Supplemental Tables 2, 3). Yet overall, overlap with the original home range remained high (over 80%). In contrast, the core areas used by females shifted between each consecutive period, with the proportional shift fairly consistent across periods (Fig. 3, Online Resource 1, Supplemental Tables 2, 3). There were less overlap and more shifting of core areas than home range during the cub-rearing periods. The overlap between the original (solitary before) and cub-rearing core areas was low (averaging 54%) and remained low even after cubs had dispersed (Fig. 3).

There was a high overlap of both home range and core areas between the period prior to giving birth and the first 4-month cub-rearing period (Fig. 4); i.e., even though home range size and core areas contracted significantly immediately after giving birth (Fig. 2), the areas used were mostly within the original home range and core areas (Fig. 3). After that, the overlap of home ranges and core areas dropped significantly between consecutive periods; i.e., females with cubs were remaining primarily within original home ranges (Fig. 2), but shifting areas of use within the home range (Online Resource 1, Supplementary Fig. 1), with overlap less than 50% of core areas from the previous 4-month period (Fig. 4). The smallest overlap occurred between the first and second

Fig. 3 Proportional overlap of home ranges and core areas between the period when ten Amur tigresses were solitary before having cubs and the cub-rearing periods (with cubs in months 0–4, months 5–8, months 9–12, and months 13–18) and the period when females were solitary after cubs dispersed in and around Sikhote-Alin Biosphere Reserve, Russian Far East, 1992–2010
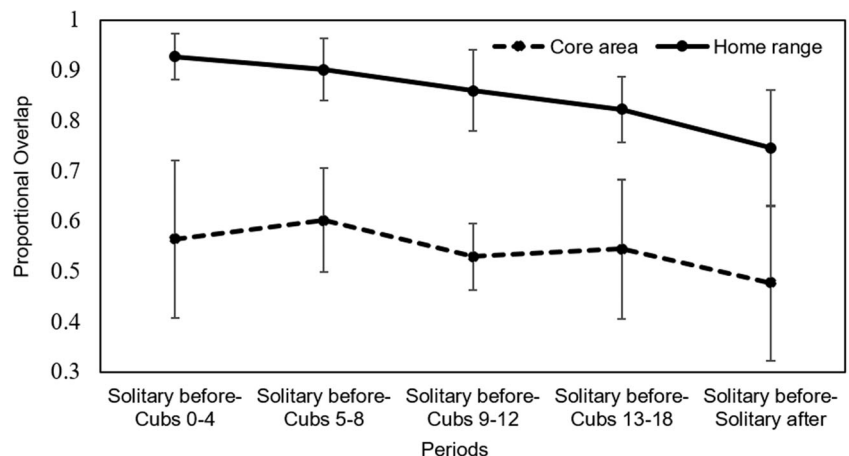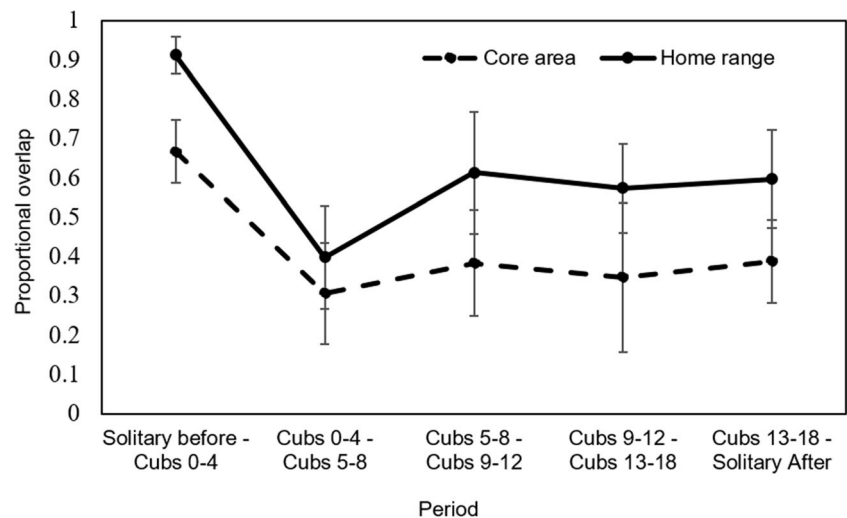
Fig. 4 Proportional overlap of home ranges and core areas between consecutive periods when ten Amur tigresses were solitary before having cubs, during the cub-rearing periods (months 0–4, months 5–8, months 9–12, and months 13–18) and the period when females were solitary after cubs had dispersed in and around Sikhote-Alin Biosphere Reserve, Russian Far East, 1992–2010

cub-rearing periods. Subsequently, the overlap between consecutive periods remained relatively stable, but low, for both home ranges (approximately 60% overlap) and core areas (30–40% overlap).

Changes in home range size

We identified four instances (3 females) in which home range size declined after the dispersal of cubs; in all cases, females had daughters in the litter when a decline occurred, and in all cases, we were able to confirm or had sufficient evidence to believe that philopatry was associated with the decline (F03, F04, and F35 in two instances; Online Resource 1, Supplemental Table 1). In two cases, radio-collared mothers and daughters were monitored throughout the entire process (Fig. 5). In other cases, collars failed or individuals disappeared before the entire process was complete. For all three females, the maternal home range size shrunk by an average $43\% \pm 18\%$ after philopatry (for one female this represents the difference from before the first and after the second litter). In the fifth case of philopatry, home range and core area location of F37 (litter 2) shifted, but home range size did not change (Fig. 5c, d; Online Resource 1, Supplemental Table 1). We found no evidence of females losing territory to an intruding female while rearing cubs.

We documented four instances in which home range size was very large, averaging 775 ± 106 km^2. In two of these cases, we found evidence that a mother allocated a portion of her home range to the daughter(s) of the subsequent litter (Fig. 6). In the first case, two daughters obtained portions of the maternal home range, while the mother's home range (F03) declined from 644 to 269 km^2 (Fig. 6). In the second case, we observed home range decline of the mother (F04) at the end of the cub-rearing cycle (from 875 to 234 km^2), at which time F04 disappeared. Her daughter subsequently acquired the entirety of her mother's home range (Fig. 6). In the

third case, the collar on the mother failed (F32) after acquiring a larger home range, and in the fourth case, the mother was poached shortly after she increased home range size (F01).

Discussion

The results of our study indicate that the reproductive status of wild Amur tiger females has a major influence on size and spatial dynamics of their home range and core area. We observed a 60% decrease in home range size associated with the birthing of cubs following by an incremental recovery of the original home range and core area throughout the 18-month cub-rearing period. A reduction of home range size coinciding with birthing has been reported before (Maehr et al. 1989; Bailey 1993; Schmidt 1998; Odden and Wegge 2005; Criffield et al. 2018), but the duration of time needed to regain their original home range had not been documented. These changes seem to coincide at least partially with physical development of cubs, and their capacity to cover greater distances. During the first 2 months after birth, tiger cubs remain at the den site, and a female's capacity to travel is severely restricted by the need to protect and feed cubs (Petrunenko et al. 2019). When cubs leave the den site (usually at about 2 months), the female brings cubs to kill sites, but is still restricted by the limited mobility of young cubs. As cubs develop, the area used by females expands, but it requires the full cub-rearing cycle (18 months) for the home range to return to its original size. Changes in core areas exhibited the same pattern but the proportional collapse and recovery of core areas were less dramatic.

The average number of locations used to estimate home range and core area size was within the range Goodrich et al. (2010) identified an asymptote (45 + 9) for defining kernel-estimated parameters. Sample size for solitary periods was on average larger due largely to the greater length of

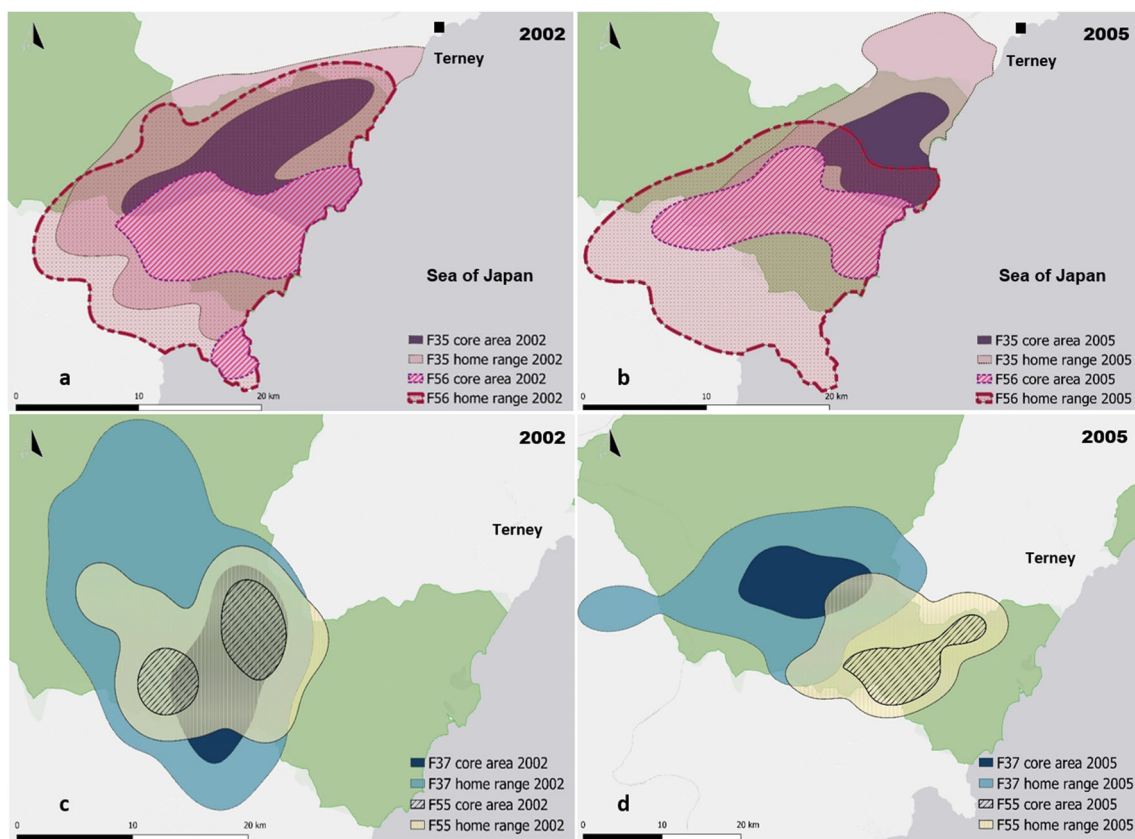**Fig. 5** Spatial overlap of mothers and daughters in 2002 and 2005: **a** F35 and her daughter F56 in 2002 when F56 was 15.5–18 months old. F56 occupied 89% of her mother's home range and 32% of her mother's core area; **b** F35 and her daughter F56 in 2005. F56 inherited about 80 km² of her mother's home range and settled in its southern portion. Despite high overlap of home ranges (50%), core areas were nearly completely separate (6% overlap); **c** F37 and her daughter F55 in 2002, when F55 was 14.5–18 months old. F55 occupied 48% of her mother's home range and her core area encompassed 30% of her mother's core area; **d** F37 and F55 in 2005. F55's home range overlapped only 19% of her mother's home range and core areas did not overlap

solitary periods, while approximately 20% of cub-rearing periods were derived from sample sizes of less than 20. We used the continuous intervals from the time when females were considered "adults" (3 years old) and without cubs to estimate home range size when females were solitary. We used longer intervals for solitary females to preserve potentially important information about how females used their home range when without cubs and obtain more precise estimates (through larger sample size). Small sample sizes for some estimates were likely responsible for much of the variability in home range boundaries between periods and likely resulted in overestimates of home range size in some cases. Therefore, the shifting boundaries of home ranges are likely at least partly an artefact of small sample size. However, the shifts (i.e., low overlap) of core areas both between the original core and cub-rearing periods, and amongst consecutive cub-rearing periods, were greater than for home ranges and statistically significant, suggesting that while the boundaries of home ranges may have shifted little, changes in core area location were frequent and real. Hojnowski et al. (2012) demonstrated that Amur tigresses do not demonstrate seasonal shifts to track

changing prey distribution, suggesting that the shifts we detected in core areas likely reflect the varying habitat requirements and ecological constraints during the cub-rearing process.

Female Amur tigers tend to select den sites that are remote, high elevation rocky areas, apparently to reduce the risk of predation (Seryodkin et al. 2012): these areas are less likely to be visited by male tigers or other carnivores, and the rocky formations provide small crevices where cubs can hide from larger predators. These unique requirements exist only during the first 2 months after birth, after which cubs leave den sites permanently and core areas began to shift regularly. We hypothesized that because of these unique constraints, core areas before and immediately after birth may overlap little. However, our results demonstrated just the opposite: females demonstrated the highest fidelity to their original core area during the first 4-month cub-rearing period, suggesting that appropriate den sites are perhaps not difficult to find within core areas, or perhaps that core areas develop with the existence of den sites included as a parameter of importance. Alternatively, perhaps the need for females to be efficient
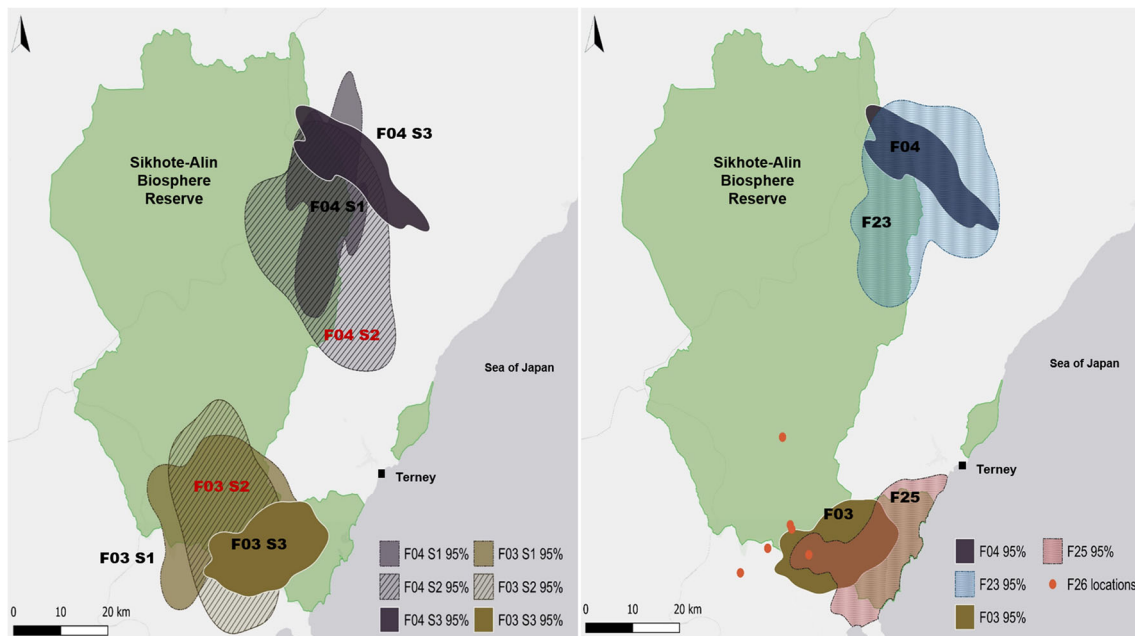
Fig. 6 **a** Contraction of maternal home range size associated with allocation of land to daughters of Amur tigresses, Sikhote-Alin Biosphere Reserve. After the second litter (period S3), home range size declined; **b** As home range size of F03 declined, her daughters (F25 and F26) established home ranges that incorporated parts of their natal home range (insufficient data to plot home range of F26). F04's home range collapsed 42% (from period S2 to S3) when her daughter, F23, was 12–18 months old. F04 then disappeared, and F23 inherited most of her mother's home range

hunters with newborn cubs (to minimize time away from the den site; Petrunenko et al. 2019) is of critical importance, and by selecting birthing sites within the core area, females can focus hunting where they are most knowledgeable of prey distribution and vulnerability (Petrunenko et al. 2016).

Our results indicate that while home range boundaries shift very little, concentrated use within the home range (core areas) shifts substantially, although these shifts occur only as the mobility of cubs increases. These results contradict earlier suggestions that core areas of tigers are stable (Hernandez-Blanco et al. 2015) and contradict the notion that there is a single, most important core area within a breeding female's home range. Consistent changes in core areas over the cub-rearing process may allow females to exploit prey in different sectors of her home range over time. Such shifts may not be noticeable in more productive ecosystems, where home ranges of tigresses are small, but may be an important strategy where prey densities are low and home ranges large. More detailed analyses of movements, prey abundance, and predation patterns would be needed to verify this hypothesis.

We found no evidence of females losing territory to an intruding female while rearing cubs, but home ranges of three females contracted a total of four times at the end of the cub-rearing process. In all cases, mothers had female offspring, and we were able to confirm or had some evidence to suspect daughters inherited a portion or the entirety of the maternal home range. In an additional case of philopatry, a shift in location occurred, but there was no decline in the size of the

maternal home range. In three of the four instances when females allocated a portion of their home range to daughters, they did not relinquish a large portion of their core area, suggesting that they retained the most commonly used portion of their home range.

Fattebert et al. (2016) suggested that there exist at least two competing hypotheses to explain spatial relationships of solitary female carnivores. Sandell (1989) hypothesized that females acquire minimum space needed for the most critical period of the year (which for most females would be rearing of cubs). Alternatively, Fattebert et al. (2016) argued that females will acquire "surplus" lands when possible to be able to allocate land to female offspring. We suggest that these are not competing hypotheses, but complementary, as they both explain behavior of tigresses under varying social conditions. We observed spacing of female home ranges that seemed to support both the space minimization hypothesis and the home range expansion-philopatry hypothesis. We identified instances in which home range size increased and were able to document inheritance of maternal home ranges, or a portion of them, by daughters, in agreement with Fattebert et al.'s (2016) hypothesis. But we also saw great stability in home range size in general, through multiple litters for some females, as predicted by Sandell (1989). However, changeover of female home ranges was common in our study area, largely due to poaching (Goodrich et al. 2008, 2010; Robinson et al. 2015). Even though prey resources were relatively stable and evenly distributed over much of our study period (Stephens et al.

2006), the frequent disappearance of females provided opportunities for daughters to acquire home ranges adjacent to their mothers, and for mothers to acquire additional land to later allocate to daughters, as proposed by Fattebert et al. (2016), and as noted earlier by Goodrich et al. (2010). A similar situation would occur when a carnivore population is not at carrying capacity. However, if female densities were at carrying capacity with low turnover, we would expect more territorial conflict, as reported by Smith et al. (1987) in Nepal, where increases in home range size were not reported, and expansion of home range by females appeared to be constrained by adjacent neighbors, as suggested by Sandell (1989).

We were not able to document any attempts to usurp territory from females during the cub-rearing process. This is somewhat surprising given the long period (a full 18 months) required by mothers to recover the entire home range. However, given the low density of tigers in our study area, our inability to track all individuals at all times, and the relatively rapid turnover of females, it is possible that such attempts were rare or could have occurred unnoticed. If such incursions did occur, however, they were apparently unsuccessful, as we found no evidence of reductions in home range size that did not appear to be associated with philopatry (Goodrich et al. 2010).

Our study provides a better understanding of the spatial dynamics of reproducing tigresses and suggests there are significant differences in how females exploit their home range with and without cubs. Cub-rearing is obviously critically important to population persistence, and tigresses face multiple constraints while rearing cubs: defense of cubs, the need to increase kill rate and/or prey size; obtaining more prey from smaller areas, and potentially having to reclaim temporarily abandoned sections of their home range from encroaching females. The time taken for females to recover home ranges while with cubs was unexpected and is likely not an issue in landscapes where home ranges are smaller, e.g., Smith et al. (1987) and Barlow et al. (2011), and can easily be traversed even when cubs are young. However, when prey densities are low, and home ranges large, the pattern and constraints we considered may be important both for other tiger populations and other large carnivore species. In particular, the long lag period in recovering a home range may have consequences when portions of territories are not defended by solitary females. We hope other studies will provide additional information to address this issue.

Data availability The datasets analyzed during the current study are available from the corresponding author upon reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Animal welfare statement For this study, we obtained data from 10 radio-collared wild Amur female tigers captured between February 1992 and December 2011 within the boundaries of Sikhote-Alin Biosphere Zapovednik. Tigers were captured in leg-hold snares or darted from a helicopter, anesthetized with ketamine mixed with xylazine or medetomidine (Goodrich et al. 2001), or with Zoletil (Lewis and Goodrich 2009), and fitted with standard very high frequency (VHF) radio-collars (Telonics, Mesa, AZ, USA). The leg-hold snares were checked at least once a day, and where possible, transmitters were placed on snares to activate upon capture. Animals were monitored (respiration rate, body temperature, and pulse) throughout the handling process, as body measurements were taken, blood collected, and radio-collars attached. After the procedure was completed, an animal a received reversing agent (if medetomidine was used) and released. Capture teams were commonly assisted by licensed veterinarians. No animals were transported or otherwise removed from their natural environment. Research on wild tigers followed American Society of Mammalogist Guidelines and was approved by the Wildlife Conservation Society's Animal Care and Use Committee.

Code availability All data analyses were performed using open source R and QGIS software, custom cods available for sharing upon reasonable request.

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