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Dale Miquelle
Wildlife Conservation Society, Bronx, NY, dmiquelle@wcs.org

Evgeny N. Smirnov
Sikhote-Alin Biosphere Zapovednik Terney, Primorskii Krai, Russia

Olga Yu. Zaumyslova
Sikhote-Alin Biosphere Zapovednik Terney, Primorskii Krai, Russia

Svetlana V. Soutryina
Sikhote-Alin Biosphere Zapovednik Terney, Primorskii Krai, Russia

Douglas H. Johnson
USGS Northern Prairie Wildlife Research Center, Saint Paul, Minnesota, Douglas_H_Johnson@usgs.gov

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POPULATION DYNAMICS OF AMUR TIGERS (*P. t. altaica*, Temminck 1884) IN SIKHOTE-ALIN ZAPOVEDNIK: 1966-2012

Dale MIQUELLE[1] Evgeny N. SMIRNOV[2], Olga Yu. ZAUMYSLOVA[2], Svetlana V. SOUTRYINA[2] and Douglas H. JOHNSON[3]

[1]Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY

[2]Sikhote-Alin Biosphere Zapovednik Terney, Primorskii Krai, Russia

[3]USGS Northern Prairie Wildlife Research Center, 204 Hodson Hall, 1980 Folwell Ave., Saint Paul, Minnesota 55108

[†] Corresponding author. Dale Miquelle, Phone: +7-924-243-6800 (Russia), email: dmiquelle@wcs.org

Running title: Population dynamics of Amur tigers

Abstract. The world's tiger (*Panthera tigris*, Linnaeus 1758) range countries agreed to double tiger numbers over twelve years, but whether such an increase is biologically feasible has not been assessed. Long-term monitoring of tigers in Sikhote-Alin Biosphere Zapovednik (SABZ), Russia provided an opportunity to determine growth rates of a recovering population. A 41-year growth phase was followed by a rapid decline in tiger numbers. Annual growth rates during the growth phase averaged 4.6%, beginning near 10% in the earliest years but quickly dropping below 5%. Sex ratio (females per male) mirrored growth rates, declining as population size increased. The rapid decline from 2008 to 2011 appeared to be tied to multiple factors, including poaching, severe winters, and disease. Reproductive indicators of this population are similar to those of Bengal tiger populations, suggesting that growth rates may be similar. Five conclusions relevant to tiger conservation are: 1) tiger populations likely in general grow slowly – 3-5% yearly increases are realistic and larger growth rates are likely only when populations are highly depressed, mortality rates are low, and prey populations are high relative to numbers of adult females; 2) while more research is needed, it should not be assumed that tiger populations with high prey densities will necessarily grow more quickly than populations with low prey densities; 3) while growth is slow, decline can be rapid; 4) because declines can happen so quickly, there is a constant need to monitor populations and be ready to respond with appropriate and timely conservation interventions if tiger populations are to remain secure; and 5) an average annual growth rate across all tiger populations of 6%, required to reach the Global Tiger Initiative's goal of doubling tiger numbers in 12 years, is a noble but unlikely scenario.

Key words: Amur tiger, population dynamics, growth rates

INTRODUCTION

Even though the tiger (*Panthera tigris*, Linnaeus 1758) is unlikely to go extinct in the wild in the immediate future, its current trajectory is catastrophic. Faced with an exploding human population and associated development booms across many of the Asian countries where they occur, tiger populations have plummeted from an estimated 100,000 in the beginning of the 19th century to no more than 3,500 today (Seidensticker 2010). Habitat loss and poaching of tigers and their prey has resulted in dramatic losses across their range. Tigers now occupy 7 percent of their historical range, and in the past decade, the area occupied by tigers has decreased by an estimated 41 percent (Dinerstein 2006). In short, Asia's most iconic species is in trouble.

If tigers are to survive, governments throughout the species' range must demonstrate greater resolve and lasting commitments to conserve tigers (Dinerstein et al. 2007). To generate such a response, the Global Tiger Initiative was created, a partnership of 13 tiger range countries, the World Bank, and multiple non-governmental organizations. At the International Tiger Forum ("Tiger Summit"), held in St. Petersburg Russia, November 21-24, 2010, range countries committed to the Global Tiger Recovery Program (GTRP), which includes country-specific recovery projects across the entirety of the tiger's current range. Of the many commitments made by country governments to conserve tigers, perhaps the most widely publicized has been the goal of doubling wild tiger numbers (publicized as "2xT") across their range by 2022 (Global Tiger Initiative Secretariat 2010).

While the stated goal of the GTRP (2xT) is praiseworthy, there is actually very little known about population growth rates of tigers, and whether a doubling of tiger numbers is even biologically possible within a 12-year timeframe. The time it takes a population of any sort to double is well defined: $t = \ln(2)/r$, where t is time in years and r is the instantaneous rate of increase (Dinsmore and Johnson 2012). If $t = 12$, growth rates must be greater than 5.77% per year, or approximately 6%. Therefore, a fundamental question facing the Global Tiger Initiative is whether the global tiger population can increase on average at 6% per year over a 12-year period beginning in 2010.

Many biologists consider tigers to be "prolific breeders" and suggest that tiger populations can grow quickly if properly protected and adequate prey exist (Karanth & Stith 1999, Sunquist et al. 1999). In contrast, Chapron et al. (2008) suggested just the opposite: that age of first birth and inter-birth interval for tigers are some of the largest of the felids, and consequently tigers will, in general, have slower growth rates than other large felids.

However, aside from modeling attempts (Karanth and Stith 1999, Kenney et al. 1995, Chapron et al. 2008) and anecdotal accounts, the only published estimates we are aware of on tiger population growth rates come from Nagarhole National Park, India, where Karanth et al. (2006) estimated a 3% growth rate over a 5-year period, and from Sikhote-Alin Reserve, Russia, where Smirnov and Miquelle (1999) reported a 6% growth rate over a 28-year period. These later results would seem to suggest that a 6% growth rate is a reasonable assumption for the GTRP to make, especially considering the estimates came from a northern, presumably less productive environment. However, growth rates of any wildlife population will depend on the complex interactions of reproduction rates, mortality rates, immigration and emigration. An understanding of how these parameters vary between populations and over time would provide some insight into expected growth rates of any recovering tiger population.

Population monitoring in Sikhote-Alin Biosphere Zapovednik (SABZ) began in 1966, when two tigers appeared in the reserve after a localized extinction (Smirnov and Miquelle 1999). Consistent monitoring documented the recovery of this population, and has continued to present, providing an opportunity to assess how growth rates might vary over time with a recovering tiger population. Because monitoring began at a time when tigers had been locally extinct in SABZ, but protection was strong, initially the population was presumably growing without any major environmental constraints. We can thus devise an estimate of the maximum potential growth rate (r_{max}), often referred to as the intrinsic rate of growth, which is defined formally as the rate at which a population with a stable age distribution would increase if no resource were limiting (Caughley and Gunn 1996). But growth rates likely change over time, with density dependent mechanisms possibly limiting growth in the later stages (Dinesmore and Johnson 2012). By looking at changes in growth rate over time for tigers in SABZ we may gain insight into likely growth scenarios for tiger populations in general, and may better project potential growth rates for recovering tiger populations across their range, and thereby may better assess the feasibility of the GTRP goal of doubling tiger numbers in 12 years.

Because reproduction rates are considered one of the most important factors affecting growth rates, we also attempt to look at variation in this parameter over time. Reproduction rates are often considered to be high in tiger populations with high prey densities (Karanth and Stith 1999), suggesting that tiger populations living in more productive regions should demonstrate higher growth rates than, for instance, tigers in Russia. Therefore, a comparison of reproductive rates across sites is also warranted, as evidence of large variations would suggest that population responses to conservation interventions may vary greatly depending on local conditions.

Our objectives in this paper are to: 1) derive an estimate of the maximum potential growth rate of tigers by looking at growth rates in the initial phases of recovery of the SABZ tiger population; 2) estimate growth rates at different points in the recovery process of the SABZ tiger population; 3) assess variation in reproduction rates across the range of tigers to determine the extent of variation under different conditions; and, 4) estimate expected growth rates of recovering tiger populations, and under what conditions might a doubling of tiger numbers be feasible.

MATERIALS AND METHODS

Study Area

Sikhote-Alin State Biosphere Zapovednik is located in northeast Primorskii Krai (Province), Russia (Fig. 1). Size of SABZ has changed dramatically over time. When first created in 1935, it was 10,588 km^2, but in 1951 the Zapovednik was reduced to its zenith of 1000 km^2. In 1966 (when estimates of tiger numbers began) the Reserve was 3101 km^2, but since then it has changed size 6 times: 2843 km^2 in 1967; 2787 km^2 in 1968; 2735 km^2 in 1971; 3402 in1974, 3471 km^2 in 1978; and finally, to its current size, 3872.8 km^2, in 1996. Portions of SABZ border the Sea of Japan, but its central feature is the Sikhote-Alin Mountains, a low range (most peaks are below 1200 m) which parallels the Sea of Japan and bisects Primorskii and Khabarovskii Krais. Sikhote-Alin Zapovednik is situated close to the center of the existent Amur tiger population (Matyushkin et al. 1996, Hebblewhite et al. 2014) and tigers in the reserve are part of that larger Sikhote-Alin Mountain ecosystem population, with nearly continuous forest cover along its border providing full connectivity with the larger population.

Population size

Information on distribution and status of Amur tigers in SABZ has been collected since creation of the protected area in 1935 (Matyushkin et al. 1981). Researchers derived expert assessments of tiger numbers based on the few tracks found from 1966-1970. After that a more formal count with a well defined methodology has been conducted on a yearly basis. These methods are detailed in Smirnov and Miquelle (1999), Miquelle et al. (2006) and Stephens et al. (2006) and are briefly reviewed here. Annual surveys are conducted along 300-400 km of permanently established transects (with total km surveyed expanding with increases in reserve size) 1-3 times per year after recent snowfall. Location, number and size of all tiger tracks are recorded. All records from each winter count and other reports are tabulated chronologically and by area.

Tracks of tigers are allocated to one of 4 sex and age categories based on the width of the pad on the front paw (Abramov 1961, Matyushkin and Yudakov 1974, Yudakov and Nikalaev 1987, Matyushkin et al. 1996; Kerley et al. 2005): tigers with pad widths equal to or greater than 10.5 cm are considered adult/subadult males (male pad width reaches 10.5 cm, i.e., larger than adult females, usually by 15-18 months) (Kerley et al. 2005); pad widths between 8.5-10.5 were considered adult/subadult females; and pad widths below 8.5 were considered cubs. Where tracks from groups of tigers were encountered and tracks of at least one individual were greater than 8.5 cm, it was assumed to be a female with cubs. A fourth category, undetermined sex-age ("unknown"), is used for tracks that could not be measured due to snow conditions or age of the track, but unless there is contradictory evidence, these tracks are assumed to be made by adults/subadults of unknown sex.

Population size and structure were derived (by authors) by estimating the number of individuals in the study area, overlapping and adjacent individuals being distinguished by size of tracks and their temporal-spatial distribution (Smirnov and Miquelle 1999, Miquelle et al. 2006). Multiple observations of similar-sized tracks in an area that approximates one home range are considered one individual. Females with cubs are the most distinctive group due to track size and consistent group size, and therefore provide a check on estimating frequency of repeated track sightings of specific individuals. Where interpretation of tracks is unclear, a range of values are reported to represent the potential number of animals (e.g., Table 1). For analyses, we used the mean value of that range for any given year.

In January 2009 record snowfalls prevented surveyors to cover many of the standard routes, and greatly restricted movements of ungulates and tigers (based on snow tracking and radio-collared tigers, unpubl. data). Consequently, survey results for this year clearly represented an underestimate of the actual number of tigers in the reserve. We corrected this estimate by our best estimate of the existent population, based on information acquired prior to and after survey periods (using camera traps, radiocollared individuals, and track data).

Because the winter surveys were not instantaneous (data are collected over 3-4 months), some mortality and natality may occur during the count period, violating the assumption of population closure for the survey period. However, most births occur outside the winter survey period (Kerley et al. 2003), and the bias associated with mortality should have been normally distributed over all years, thereby not substantially biasing estimates of growth rate.

We believe this survey methodology is conservative in estimating population size because: (1) there is a probability of missing tracks of individuals, especially in remote sections of SABZ; and, (2) repeated reports of tracks in an area are conservatively interpreted, i.e., tracks of similar size temporally separated in one drainage will usually be attributed to one individual, when in fact they could theoretically be made by 2 or more. Though statistical confidence limits cannot be applied to the count method, a range of values is given for each sex and age group for each year that reflects the uncertainty of interpreting existing records. Because the same methodology has been applied throughout the entire period of study, we believe the values accurately reflect trends in population size and structure, although error is clearly associated with an unknown level of detectability. Comparisons to estimates based on radio-collared tigers and camera trapping in Sikhote-Alin Zapovednik (Soutyrina et al. 2013) generally support the interpretations of population structure and size reported here.

Because size of the reserve fluctuated during the study period, we derived a density estimate as the total population $count_i$/area of the $reserve_i$, where i = year in which population size was estimated. We then estimated growth rates as $Density_i/Density_{i-1}$.

To quantify population growth and decline, we used the estimate of R_{real} (Slaski et al. 2005) to express the fractional increase or decrease in abundance from one year to the next, where

$$R_{real} = (N_t-N_{t-1})/N_{t-1}, \text{ or } \lambda - 1, \text{ where } \lambda = (N_t/N_{t-1})$$

With population density estimates, we used a smoothing procedure to reduce the yearly fluctuations in numbers associated with counting error. The "loess" regression procedure fits nonparametric curves (LOcally wEighted Scatterplot Smoothing) with a smoothing pattern that does not assume the numbers were generated by any particular statistical distribution (Cleveland 1979). The dependent variable is smoothed as a function of the independent variables in a fashion analogous to how a moving average is computed for a time series (Cleveland and Devlin 1988). A smoothing value, *f*, can increase the smoothness of the curve by increasing the neighborhood of influential points (Cleveland 1979). We calculated loess regressions in SAS, and chose the smoothing parameter value that minimized Akaike's Information Criterion, corrected for small sample size. This approach provides greater stability to yearly estimates and a better representation of local changes in the population. Because the population density was not measured with certainty, we also used the smoothed density estimates to predict growth rates of the population using the same parameter (R_{real}).

This estimate of growth rate using the smoothed density estimates provides a stable and useful estimate of changes in population growth over time.

Sex ratio and reproduction parameters

Sex ratio is reported as number of females/male, and is based on the reported number of adults and subadults of each sex, with animals of unknown sex deleted from the analysis. Tracks of females with and without cubs provided estimates of reproduction rate (defined here as number of cubs/female for each year). We included cubs of all ages for this assessment, as long as they were still in association with their mother.

Yearly estimates of growth rates, sex ratio and reproduction rates for the 47 years of data were divided into 5 study periods: four periods of 10-11 years each (Period 1 = 1966-1975, Period 2 = 1976-1986, Period 3 = 1987-1997, and Period 4 = 1998-2008), and a final period 5 was selected *post hoc* to coincide with the period of population decline, starting in 2009 (2009-2012). We used the means of these five periods to examine changes in sex ratio and reproduction rates using an analysis of variance. All means are reported with ± 95% confidence intervals.

To compare reproduction parameters of the SABZ population to other tiger populations, we collated all published reports we could find on age of first reproduction of tigers in the wild, interbirth interval, and number of cubs/litter. Similar to Smith and McDougal (1991) and Singh (2013), we were not able to detect litters at birth (Kerley et al. 2003), so the derived estimates of litter size must be considered conservative.

RESULTS

Population size and density

No tigers were reported in SABZ in 1964 or 1965, suggesting a localized extinction had occurred. Recolonization of the reserve began in 1966, when 2 females, one already with a litter of one, were reported (Table 1). Total population size increased, with fluctuations, during the first 41 years of study (Figure 2). The total number of tigers (adults and cubs) peaked at 38 animals in 2005 and 2007 (Table 1, Figure 2). The peak number of adults (30) occurred in 2007.

The maximum density of the SABZ tiger population (all sex-age classes) was reported in 1995 (0.95 tigers/100 km^2). Due to an increase in size of the reserve (in an area where tigers were uncommon) and fluctuations in tiger numbers this peak density was not reached again until 2007, when maximum density of adult tigers was also reached at 0.75/100 km^2 (Table 1).

Tiger numbers began to decline in 2008, but remained above 30 until 2010, when a dramatic drop occurred, and continued through 2012, when tigers reached their lowest point (7 individuals) since 1972. Magnifying the decline, no reproduction occurred in 2011 - the only time in the 47 years of monitoring when no cubs were reported.

A locally weighted (loess) smoothing regression suggests that the tiger population increased generally in a linear fashion from 1966 to 2000 and then declined (Figure 3). While this smoothing function appears to do a good job of dealing with yearly fluctuations in tiger numbers during the growth phase, it improperly expands the period of decline back to approximately 2005, when in reality it started no earlier than 2008.

Population growth.

Over the 47 years of study the population grew on average at 4.6% ± 7.0%, with the large confidence interval an indication of the great variation in growth rates over time. While the population appeared to increase in a linear manner (Figure 3), the proportional change in tiger numbers (R_{real}) varied greatly (Figure 4). There was significant variation in the average growth rate across the 5 periods of study ($F_{4,41} = 3.21$, $p = 0.022$) but significance was driven by the last period when growth rates were negative. Even though the average growth rate varied from 0.17 (period 1) to 0.017 (period 4) the same test without period 5 showed no significant difference ($F_{3, 38} = 1.14$, $p = 0.346$) because of the great fluctuation in yearly growth estimates. Applying the loess smoothing regression applied to the proportional change in tiger numbers (R_{real}) from Figure 4 (Figure 5) provides a much clearer picture. Growth rates were high in the early years of this study (6-10%) but dropped below 6% within nine years, and continued to drop until they reached 1% in the early 1990s.   .

Sex ratio and reproduction parameters

The sex ratio of the SABZ tiger population averaged 1.97 ± 0.23 females/male, but demonstrated a gradual but persistent decline over the study period, ranging from a high of 3.5 females/male early on (1969-1971) to a low of 0.33 females/male in 2011. This ratio decreased significantly over the five observation periods (ANOVA F= 16.01, df = 4, 42, $p < 0.0001$) (Figure 6).

Reproductive rates (Figure 7) also varied significantly by period (F= 4.61, df = 4, 42, p = 0.0003), with a peak within the two periods from 1977-1996.   Cubs averaged 37.8% + 4.2% of the total population, but values ranged widely, from 0 to 62% on a yearly basis. The increasing divergence in total population and adult population size from approximately 1984 through 1996 (Figure 2) reflects the higher reproduction rates during this period ($F = 21.0$, $df = 4, 41$, $p < 0.0001$). As growth rates slowed and then declined in the fourth and fifth observation periods (1997-2011), both sex ratio and reproductive rates declined.

Reproductive parameters of the Amur tiger in SABZ are similar to those of Bengal tigers in India and Nepal (Table 2). Age of first reproduction appears to be approximately 4 years old in all three places where it has been measured. Interbirth interval is between 21 and 25 months for 4 of 5 sites, with a notably larger interval at Ramthambore National Park in India. The estimate of cubs/litter (at first observation) in SABZ is similar to estimates in two sites in India, but lower than in Chitwan (Nepal) and Pench tiger reserves.

DISCUSSION

Population size and growth rates

The protection provided to tigers by SABZ was severely dampened in 1951 when size of the Zapovednik was cut to 1,000 km^2. Matyushkin et al. (1981) plotted the frequency of tracks within SABZ from 1957 through 1978 and reported that even though the size of the Zapovednik was restored to 3101 km^2 in 1960, the population of tigers continued to collapse and tracks completely disappeared from the reserve for three years, 1963-1965 (see Smirnov and Miquelle 1999). The localized extinction of this population was attributed to illegal hunting (new logging roads into former protected areas in the 1950's eliminated de facto protection) and continued capture of cubs. Despite supposedly tighter controls, in the winters of 1962-1963 and 1963-64, 14 cubs were captured within former Zapovednik territory. Attempts to capture cubs often resulted in death to the female. Apparently females and their cubs as well as resident males were simultaneously eliminated.

Tigers quickly reappeared in SABZ in 1966, but the process apparently represents a colonization episode. Once enforcement was reasserted, poaching of both prey species and tigers was rare through 1991 due to tight control of firearms, regular patrols of the Zapovednik, and no economic incentives (access to the international market for tiger skins and bones was virtually non-existent due to closed borders). This early recovery phase occurred in what was probably near ideal conditions for Amur tigers, with relatively high prey densities relative to tiger numbers, minimal human impact, and with emigration into the reserve an additional likely source of growth. Therefore the observed rate of increase for the Sikhote-Alin Zapovednik population during that initial phase (>10%) is probably close to the maximum rate of increase that might be expected, i.e., close to the intrinsic rate of increase (Dinesmore & Douglas 2012) Such growth rates are likely to occur only when populations are well below carrying capacity, meaning there is abundant prey relative to tiger numbers (especially females – see below), and when anthropogenic sources of mortality (most importantly poaching) are minimized.

Growth rates declined continuously through the 1970s towards 5% (Figure 4), and continued to drop (below 5%) in the 1980s. The collapse of the Soviet Union in 1991 brought increased poaching rates on prey and tigers regionally (Galster & Vaud Elliot 1999), and a noticeable drop in growth rates in SABZ occurred again during this period (Figure 5). But anthropogenic pressures were still likely lower in protected areas than surrounding, poorly protected lands, and despite worsening conditions tiger numbers continued to increase in SABZ, just at lower rates.

Because ungulate numbers were increasing during much of the growth phase of the SABZ tiger population (Stephens et al. 2005) the carrying capacity was in essence also increasing, likely prolonging higher growth rates longer than would be the case if prey biomass were stable during this entire time. Increasing prey biomass is likely responsible for such a long growth phase.

But other factors, including dispersal, may have reduced the growth rate in SABZ. Matyushkin et al. (1981) reported that the region to the north of the reserve was still uncolonized in the mid-1970's, and Pikunov (1988) reported the general region to be sparsely populated with tigers in 1985, perhaps encouraging tiger dispersal beyond the boundaries of the reserve. Even when these areas were well populated (Matyushkin et al. 1996, 1999), dispersal of radiocollared subadult males out of the reserve was common (Goodrich et al. 2008). Whether immigration to the reserve was occurring at the same rate as emigration from the reserve is unknown, but a disproportionate outward flow (e.g., from a source to a sink) would have negatively influenced growth rates of the population.

This dataset is derived from a single sub-population of tigers in the larger Sikhote-Alin landscape, and therefore extrapolation to other populations of tigers should be done with caution. Nonetheless, we suspect the growth rate estimates derived for SABZ population may be applicable to many other tiger populations – not just in Russia but across Asia. It is often assumed that growth rates of tigers in more productive, southern environments must be higher because prey densities are often an order of magnitude greater. However, in reviewing what is known about reproduction rates, mortality rates, immigration and emigration (the sum of which determines growth rates) suggests otherwise. Our comparison of standard reproduction indices (Table 2) shows few differences between tiger populations in India and

Nepal versus SABZ. While there is variation in reproduction parameters in the Indian subcontinent, and errors associated with some parameters (e.g., litter size at birth and cub survival are poorly known) a clear difference in reproductive rates between southern and northern populations is not apparent. Mortality factors have been well studied in the SABZ population (Robinson, this issue) but similar data is absent from the Indian subcontinent. Hence while comparison of mortality rates is not possible, available evidence suggests human-caused mortality is likely the predominant factor, and likely also independent of prey density. Both SABZ and most Bengal tiger populations are in protected areas, where densities are higher than surrounding lands, and hence immigration will mostly be out of these core areas. Consequently, in considering these three factors that determine population growth (reproduction, mortality, immigration-emigration) we see little evidence that growth rates of tiger populations will be greater in more southern latitudes than the rates we have determined for the SABZ population. If this is the case, managers across Asia must recognize the limitations to growth for tiger populations, and be prepared for relatively slow recovery processes.

Differences in prey densities may not have as dramatic an impact on reproduction rates of females as intuition might suggest. Home range size of adult female tigers appears to "calibrate" to prey density, so that prey biomass per adult female home range might be similar across tiger range (Miquelle et al. 2010), suggesting that the number of prey available to each reproducing female may be similar despite varying overall prey densities, making prey density per se a poor indicator of reproductive rates, and prey abundance per adult female a better indicator. Consequently, we suggest that there is little evidence that growth rates of other tiger populations are likely to greatly exceed what has been observed in the SABZ population, and Karanth et al.'s (2006) estimate of a 3% growth rate in Nagarhole National Park, India provides some support for this assertion.

These results suggest that where recovery or reintroduction might be proposed, it seems likely that initial growth rates of 10% or slightly higher per year could be expected if prey biomass is high relative to adult female tiger numbers, and sources of human mortality are held in check. However, for populations where tigers already exist, for populations that have already been recovering for some time, or where prey densities have been depressed relative to adult female tiger numbers, growth rates will be considerably less, with 3-5% annual increases a reasonable target.

The rapid decline that occurred after 2008 in SABZ was probably caused by multiple factors, and is considered in more detail by Martin et al. (this issue) and Robinson et al (this issue). Record snowfall in January 2009 (over 2 m) may have been responsible for some tiger deaths due to their inability to travel through deep snow, but all radio collared tigers survived this event (unpubl. data), suggesting that other factors were at play. During an 18-month period (December 2009 – May 2011) we were able to document 12 deaths of tigers in the reserve. Two deaths were conclusively associated with canine distemper; 3 cubs died because their mother contracted CDC and were abandoned; 2 radio-collared tigers died of unknown causes but CDC is suspected; in a documented case of infanticide one male tiger killed two 6-month old tiger cubs and then succumbed himself after a fight with another tiger (possibly the mother); and one female that was found shot had enlarged nipples (suggesting it had cubs, and hence ensuring that at least one more cub died). These mortalities explained partially why reproduction was so low (6 known deaths of cubs) during this period (Figure 7). Although poaching is no doubt a continuing threat to this population (as revealed in the one confirmed poaching episode) a host of unusual and rare natural phenomena, as well as a potentially large impact of disease (Martin et al. this issue), were responsible for a large number of deaths in a short period. Therefore, if no further impacts of disease occur, and if poaching is controlled, we expect a relatively quick recovery of the tiger population in SAZB, with initial annual growth rates > 6%.

Population and reproduction parameters

In SABZ we found that sex ratio (females/male) declined as the population size increased. Sex ratio varies greatly for other areas and subspecies as well (Schaller 1967, Smith and McDougal 1991, Abramov 1960, Yudakov and Nikalaev 1972, Pikunov et al. 1983). The average sex ratio in SABZ (close to 2.0) is higher than other reports for Amur tigers, and our range (4:1 to 0.3:1) covers the entire range of values reported elsewhere.

We propose two explanations by which sex ratio may change in association with changes in population numbers. First, our data suggest that subadult females rarely disperse far, while subadult males will always leave the natal home range (Goodrich et al. 2010), so sex ratio would partially vary dependent on the percentage of subadult males that disperse from SABZ. In the 1960s and 1970s, when tiger populations everywhere were low, longer dispersal distances in search of breeding females may have been common since there were many "vacancies" both inside and outside SABZ. As the tiger population across the Russian Far East increased, there would have been less of a "need" to disperse long distances to find potential mates, and fewer opportunities to find vacancies outside protected areas. If more subadult males remained closer to their natal home range (and survived), this would result in a decrease in the female:male ratio. However, our data on dispersal do not provide strong evidence for this as a suitable explanation: of the five subadult males we have monitored during the later phases of this dataset (Goodrich et al 2008), four dispersed outside SABZ, suggesting that most subadult males were still dispersing far from natal home ranges.

Alternatively, the shift in female:male sex ratio could be due to more mature adult males finding a home range within the reserve. Again, when population size was low, individual males had little competition, and could possibly have ranged over larger territories, incorporating more females into their range. As population size increased, competition between males would presumably increase, and might be reflected in smaller territories, which would lead to an overall increase in adult males, and a reduction in the female:male ratio. When the sex ratio declines to a point where there are more males than females, territoriality, as documented in Sikhote-Alin Zapovednik (Goodrich et al. 2010, Hojnowski et al. 2013) may break down, at least for males, as has been documented further south in Russia (Hernandez-Blanco et al., this issue).

Reproduction rate varied from 0 to 2.6 cubs/female/year, but averages for the 5 periods of study varied substantially, with the results suggesting that reproduction rates were initially low, but increased during the middle two periods before declining, again suggesting, as with sex ratio, a density dependent phenomenon.

Conservation Implications

Between 1972 and 1977 Matyushkin et al. (1980) estimated the tiger density in SABZ to be between 0.13 - 0.32/100 km^2, and stated that such a density probably represented a maximum for the conifer-broadleaved forests of the central Sikhote-Alin Mountains. Based on data collected through 1993, we (Smirnov and Miquelle 1999) reported a much higher density (0.62/100 km^2), but also predicted that the SABZ population had attained carrying capacity sometime around 1993, and was unlikely to increase further. However, with increasing prey densities (Stephens 2005) the tiger population continued to increase to nearly 1 animal/100 km^2. In 2007 the tiger density in Sikhote-Alin was as great as that found in Lazovskii Zapovednik (0.7 to 1.4 animals/100 km^2), some 300 km to the south, a region that is considered better tiger habitat due to higher prey densities (Matyushkin et al. 1980, Zhivotchenko 1981, and Salkina 1993). Our data suggest that potential prey and tiger densities (i.e. carrying capacities) have probably been underestimated based on false assumptions that were really a reflection of the impact poaching can have (Goodrich et al. 2010, Robinson et al. this issue) both inside and nearby a protected area in artificially lowering densities of both prey and tigers.

Our data are consistent with the idea that the growth rate of the SABZ tiger population was decreasing in a density dependent manner through 2008. The decreasing growth rate over time, the decreasing reproduction rate through the past 15 years, the declining sex ratio and the relationship of growth rate to total population density suggest that “feedback” mechanisms were coming into play to reduce population growth. However, a negative relationship between density and the proportional change in population size, as seen in Figure 5, while suggestive of a density dependent relationship, may also be explained due to various mathematical artifacts (Johnson 1996). Therefore, interpretations of these data should be done with caution.

These data represent the longest continuous effort to monitor a single population of tigers in the world, and provide unique insights into the dynamics of a recovering tiger population. Estimates of growth rates derived for Sikhote-Alin and for the Nagarhole population in India suggest that 3-5% annual increases are likely to be normal for a recovering population except when tiger numbers are well below carrying capacity, at which time growth rates may reach 10% or greater for short periods. While a 10% growth rate would double numbers in less than nine years, a 3% growth rate, as measured in Nagarhole, would require 25 years before population size doubled. A consistent growth rate of 6% annually, needed to achieve the Global Tiger Initiative's goal of doubling tiger numbers in 12 years, is especially unlikely as alleviation of anthropogenic factors depressing survival and reproduction rates of tigers is presumably ongoing in this 12-year window (2010-2022), acting as a further lag effect before noticeable increases in growth rates can occur.

We believe there are five useful conclusions from these analyses relevant to tiger conservation across Asia: 1) while there are very few estimates of growth rates in tiger populations, we believe that tiger populations will in general grow slowly – 3-5% yearly increases are realistic for recovering populations in many conditions, with larger yearly increases likely only when tiger populations are highly depressed but prey density relative to numbers of adult females is high and anthropogenic sources of mortality are limited; 2) while more estimates are needed, it should not be assumed that tiger populations with high prey densities will necessarily grow more quickly than populations with low prey densities – the existent estimates of reproductive rates do not lend support to what is often intuitively assumed; 3)while growth is slow, decline of tiger populations can be rapid. 4) because declines can happen so quickly, there is a constant need to monitor tiger populations and be ready to respond with appropriate and timely conservation interventions if tiger populations are to remain secure; 5) achieving the "2xT" goal of the Global Tiger Initiative would require high growth rates across multiple tiger landscapes simultaneously, and is therefore extremely unlikely, but noble goal worth striving for.

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Table 1. Results of tiger surveys in Sikhote-Alin Zapovednik, 1996-2012 and tiger density derived from mean total numbers and size of the reserve.

Year	Adult females	Adult males	<1 yr cubs	Yearling cubs	Undetermined Sex-age	no. Litters	Total count	Zapovednik Area (km^2)	Total tiger density (#/100 km^2)
1966	2	0-1	1	0		1	3-4	3101	0.11
1967	2-3	1	2	1		2	6-7	2842.9	0.23
1968	3	1	1	2		1	7	2786.9	0.25
1969	3-4	1	2	2		1	8-9	2786.9	0.31
1970	3-4	1	2	2		2	8-9	2786.9	0.31
1971	3-4	1	0	2-3		0	6-8	2734.9	0.26
1972	3-4	1-2	1	1-2		1	7-9	2734.9	0.29
1973	4-5	2	3	2-3		2	10-13	2734.9	0.42
1974	4-5	2	1	3-4		1	10-12	3402	0.32
1975	4-5	2-3	1	4-5		1	10-14	3402	0.35
1976	4-5	2-3	1-2	3-5		1-2	10-15	3402	0.37
1977	5-6	2	5	2-3		2	14-16	3402	0.44
1978	5-7	2	2	6-7		2	15-18	3470.5	0.48
1979	4-6	2-3	0	6-8		0	12-17	3470.5	0.42
1980	5-7	2-3	6	2-4		4	15-20	3470.5	0.50
1981	6-8	2-3	2	6-8		1	16-21	3470.5	0.53
1982	5-6	2-3	5	4-6		2	16-20	3470.5	0.52
1983	5-6	3	4	2-4		2	14-17	3470.5	0.45
1984	7-9	3-4	5	5-6		3	18-24	3470.5	0.61
1985	7-9	3-4	6	5-6		4	21-25	3470.5	0.66
1986	6-8	3-4	7	5-6		4	21-25	3470.5	0.66
1987	6-8	4-5	10	5		4	22-28	3470.5	0.72
1988	7-9	3-4	4	8-10		2	19-26	3470.5	0.65
1989	7-9	4-5	5	5-6		2	21-25	3470.5	0.66
1990	8-10	3-4	4	4-5		4	20-24	3470.5	0.63
199	7-9	3-4	8	4-5		4	21-26	3470.5	0.68

1									
1992	6-8	3-5	8	10		4	27-31	3470.5	0.82
1993	7-10	3-5	10	5-6		6	24-31	3470.5	0.79
1994	10-12	6-8	7	0	2-5	4	25-32	3470.5	0.82
1995	12	5	10	2	4	8	33	3470.5	0.95
1996	8-11	6-7	9-10	5	1-2	7-8	29-35	3872.8	0.83
1997	8-12	6-8	7-8	0	5-10	4-5	26-38	3872.8	0.83
1998	8	7	5	5-6	4-5	5	29-31	3872.8	0.77
1999	7	6-9	3	5-6	6-8	2	27-33	3985.3	0.75
2000	9-10	8-9	2		5-7	1	24-28	3985.3	0.65
2001	8-9	7-8	9-10		8-9	5	32-36	3985.3	0.85
2002	9-10	7-8	5		11-12	3	33-35	3985.3	0.85
2003	9	7	13-14		6	5-6	33-36	3985.3	0.87
2004	9	6	15		7	7	37	3985.3	0.89
2005	13	10	9		6	6	38	3985.3	0.90
2006	9	7	4	1	6	2	27	3985.3	0.68
2007	11	11	4	4	8	3	38	3985.3	0.95
2008	12	7	5	2	8	4	34	3985.3	0.85
2009	3	5	3		1	2	30	3985.3	0.30
2010	11	6	2		3	0	22	3985.3	0.50
2011	2	6	0	0	7	0	15	3985.3	0.38
2012	3	3	2		1	1	9	3985.3	0.23

Table 2. A comparison of reproductive rates of tiger populations in India, Nepal, and Russia. Numbers in parentheses are sample sizes.

Parameter	Location				
	Sikhote -Alin Russia[1]	Chitwan Nepal[2]	Ramtham-bore India[3]	Pench India[3]	Panna India[4]
Age at first reproduction (yrs)	4 (4)	3.5-4.5	4.3 (11)		
Interbirth interval (months)	21.8 (7)	21.6	33.4 (7)	25.2 (9)	21.6
Cubs/litter (1st observation)	2.4	2.98	2.3 (22)	2.9 (18)	2.3 (12)

Sources: [1]Kerley et al. 2003, [2]Smith et al. 1991, [3]Singh et al. 2014, 2013, [4]Chandawat et al. 2002

Figure 1. Location of Sikhote-Alin State Zapovednik in the Russian Far East.

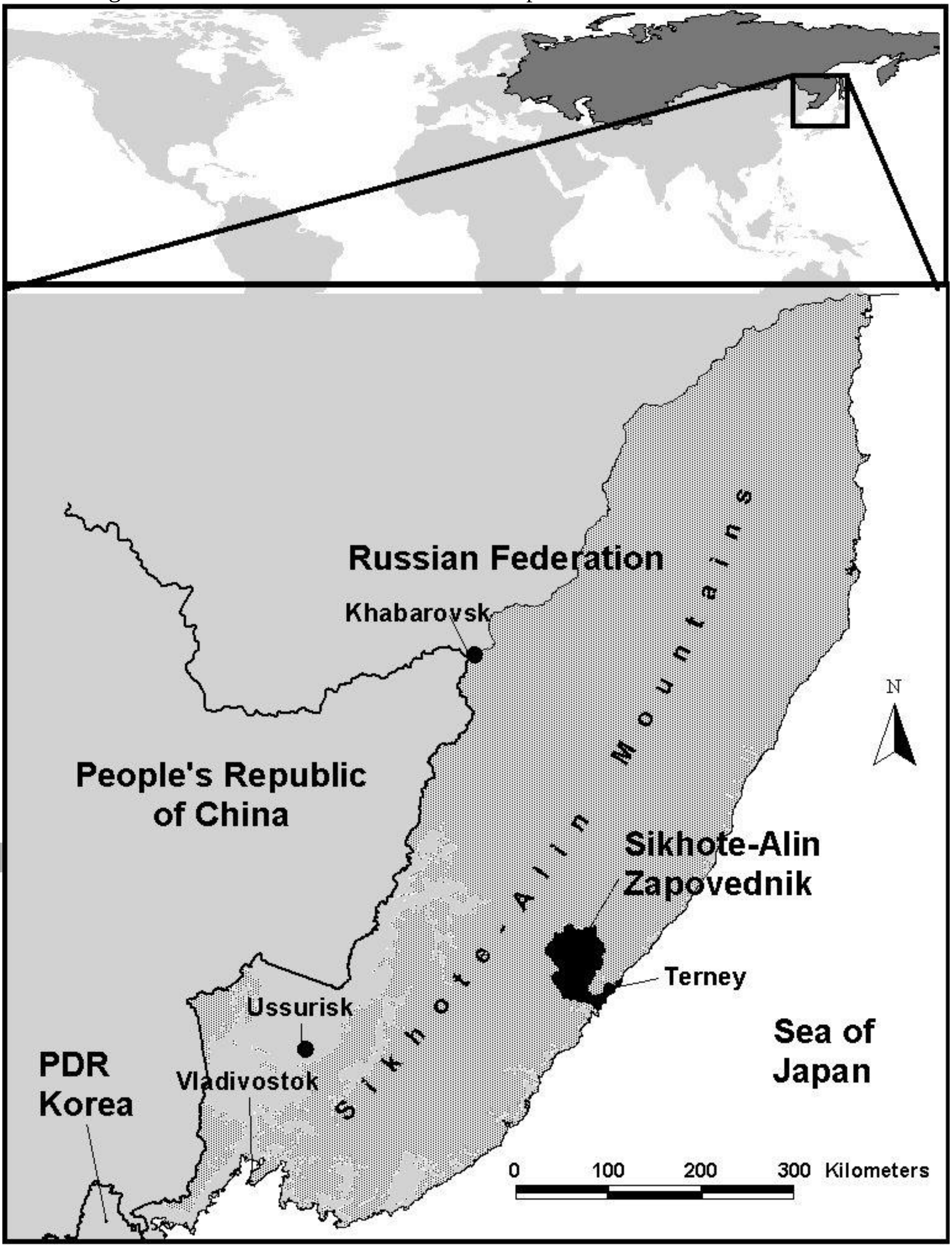

Figure 2. Yearly estimates of total population (in black) and adult population (in grey) of Amur tigers in Sikhote-Alin Biosphere Zapovednik,1966-2012.

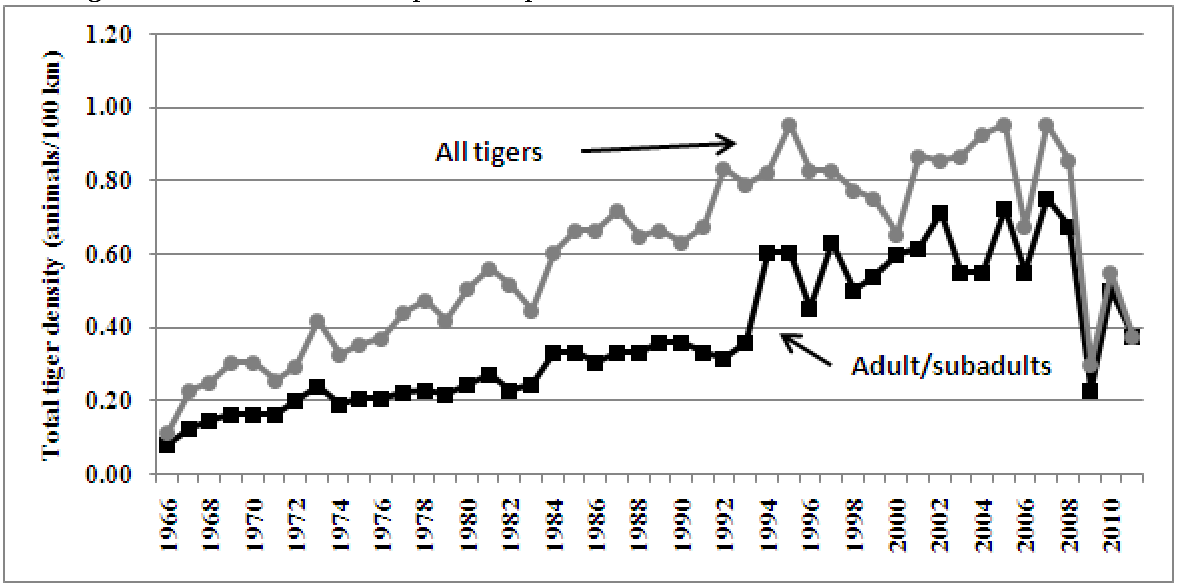

Figure 3. The smoothed loess regression represents growth of the tiger population (based on density estimates) from 1996 to 2012 at Sikhote-Alin State Biosphere Zapovednik.

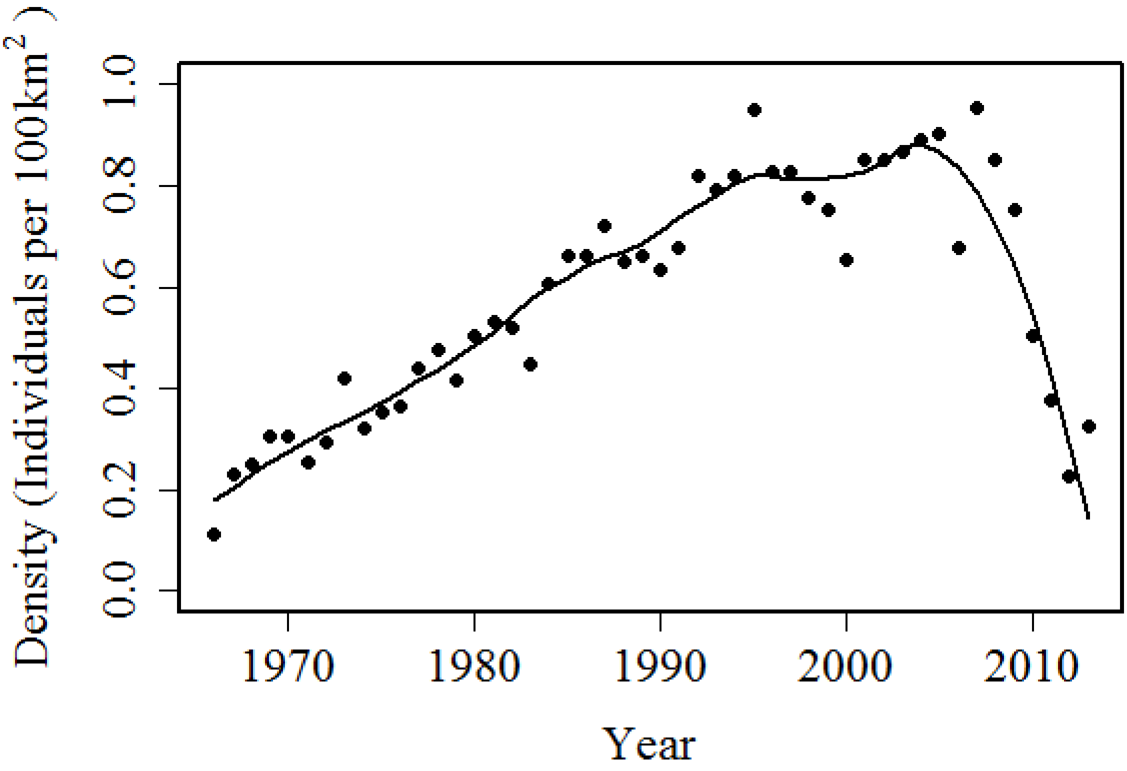

Figure 4. Proportional change in growth (R_{real}) of the Amur tiger population in Sikhote-Alin Zapovednik from 1966 through 2012.

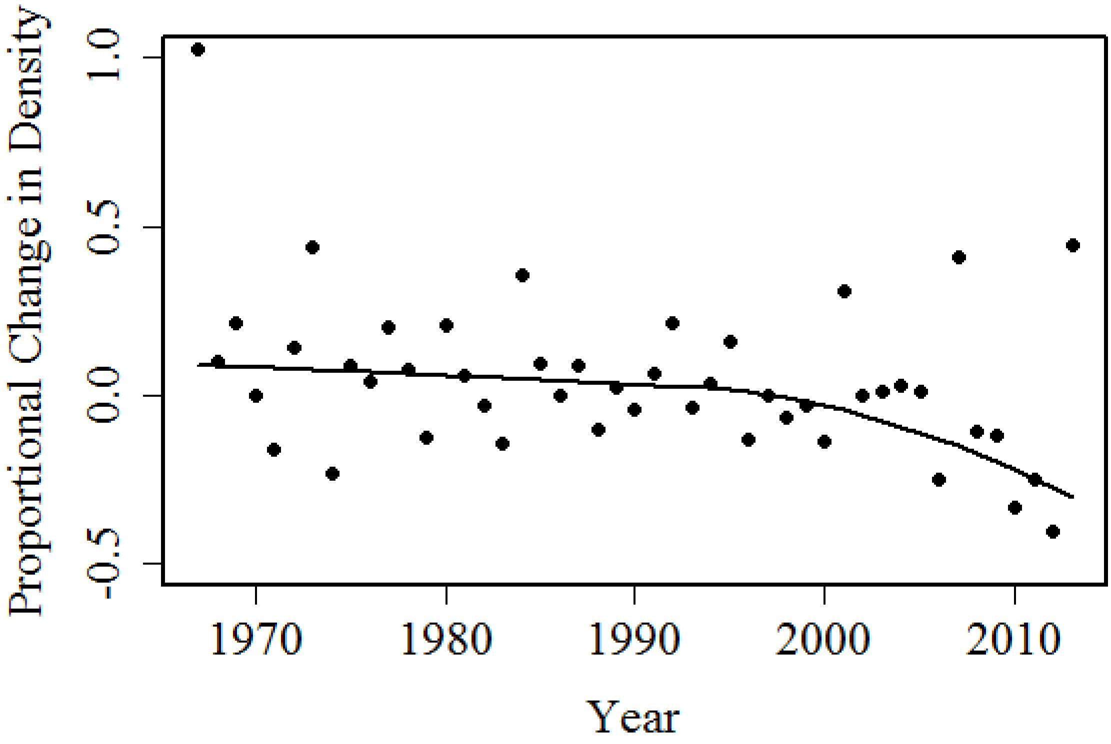

Figure 5. Estimated values of proportional change (R_{real}) in tiger numbers based on smoothed values of density (from Figure 3) of Amur tigers in Sikhote-Alin Biosphere Zapovednik,1966-2012.

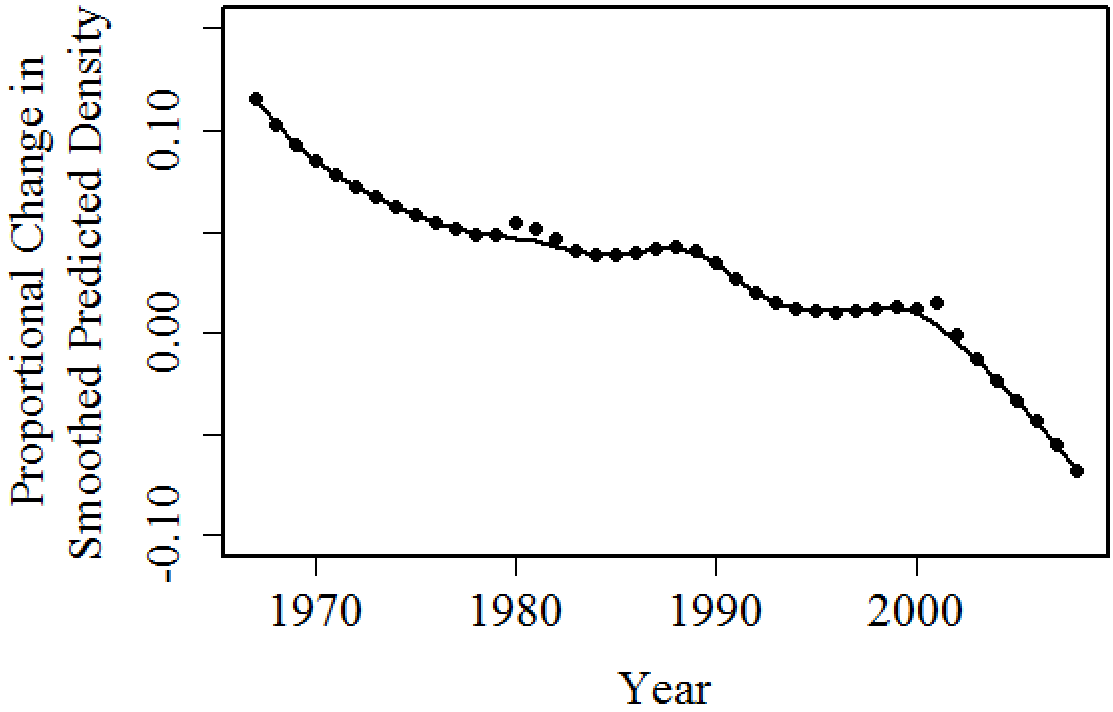

Figure 6. Sex ratio (adult females per one adult male) of Amur tigers over five periods in Sikhote-Alin Zapovednik, 1966-2012.

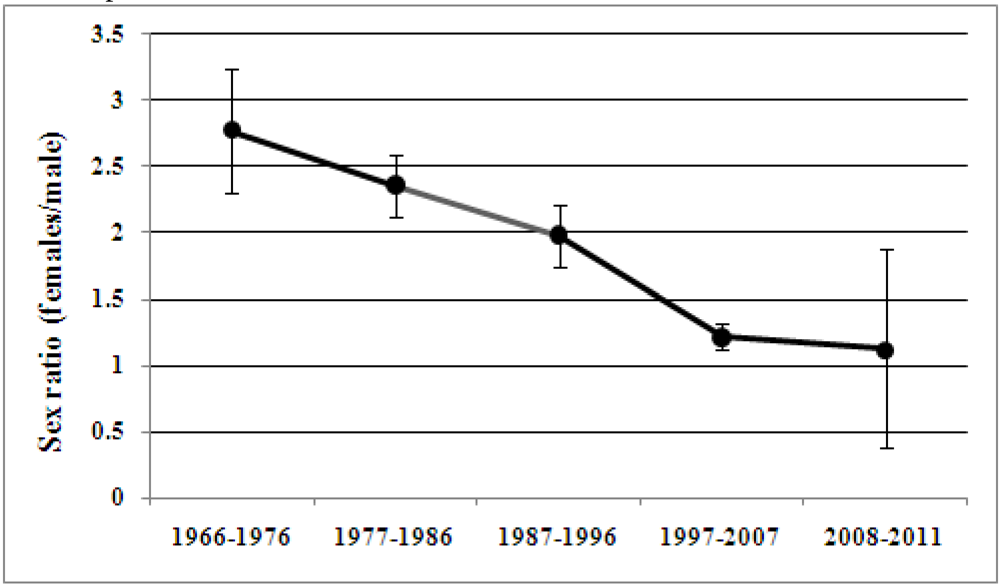

Figure 7. Reproductive rate (cubs/female/year) of tigers in Sikhote-Alin Zapovednik for five periods of observation, 1966-2012.