

ORIGINAL ARTICLE

Population dynamics of Amur tigers (*Panthera tigris altaica*) in Sikhote-Alin Biosphere Zapovednik: 1966–2012

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Abstract

In 2010, the world's tiger (*Panthera tigris*) range countries agreed to the goal of doubling tiger numbers over 12 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 2009 to 2012 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. These results suggest that, first, 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. Second, 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. Third, while growth is slow, decline can be rapid. Fourth, 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. Finally, 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, growth rates, population dynamics

INTRODUCTION

Even though the tiger [*Panthera tigris* (Linnaeus, 1758)] is unlikely to go extinct in the wild in the immediate future, its current population trajectory, if continued, would be catastrophic. Faced with an exploding human population and associated development booms across many of the Asian countries where they occur,

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tiger populations have plummeted from an estimated 100 000 at the beginning of the 19th century to no more than 3500 today (Seidensticker 2010). Habitat loss and poaching of tigers and their prey has resulted in dramatic losses across their range. Tigers now occupy 7% of their historical range, and in the past decade, the area occupied by tigers has decreased by an estimated 41% (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 commitment 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 on 21–24 November 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 "2×T") across their range by 2022 (Global Tiger Initiative Secretariat 2010).

While the stated goal of the GTRP (2×T) is praiseworthy, there is actually very little known about the 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 & 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 at 6% per year on average 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) suggest just the opposite: that age of first birth and inter-birth intervals 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 (Kenney *et al.* 1995; Karanth & Stith 1999; 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) estimate a 3% growth rate over a 5-year period, and from Sikhote-Alin Biosphere Zapovednik (SABZ) Russia, where Smirnov and Miquelle (1999) reported a 6% growth rate over a 28-year period. These later results 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 SABZ began in 1966, when two tigers appeared in the reserve after a localized extinction (Smirnov & 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. Therefore, we can 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 & Gunn 1996). However, growth rates likely change over time, with density dependent mechanisms possibly limiting growth in the later stages (Dinsmore & Johnson 2012). By looking at changes in the 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 & 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: first, to 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; second, to estimate growth rates at different points in the recovery process of the SABZ tiger population; third, to assess variation in reproduction rates across the range of tigers to determine the extent of variation under different conditions; and, finally, to 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

SABZ is located in northeast Primorskii Krai (Province), Russia (Fig. 1). The size of SABZ has changed dramatically over time. When first created in 1935, it was 10 588 km², but in 1951 the Zapovednik was reduced from its zenith to its nadir of 1000 km². In 1966 (when estimates of tiger numbers began) the Reserve was 3101 km² in size, but since then it has changed size 6 times: 2843 km² in 1967; 2787 km² in 1968; 2735 km² in 1971; 3402 in 1974; 3471 km² in 1978; and, finally, to its current size, 3872.8 km², 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 Krai. SABZ 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 to 1970. After that a more formal count with a well defined methodology has been conducted on a yearly basis. These methods are

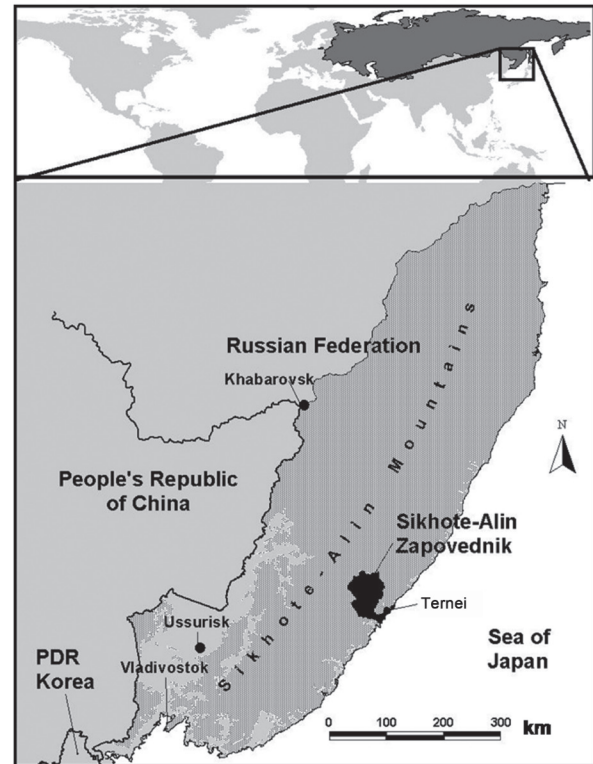


Figure 1 Location of Sikhote-Alin Biosphere Zapovednik in the Russian Far East.

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 kilometers surveyed expanding with increases in reserve size) 1–3 times per year following 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 1 of 4 sex and age categories based on the width of the pad on the front paw (Abramov 1961; Matyushkin & Yudakov 1974; Yudakov & 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); tigers with pad widths between 8.5 and 10.5 are considered adult/subadult females; and tigers with pad widths below 8.5 are considered cubs. Where tracks from

groups of tigers were encountered and tracks of at least 1 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 & Miquelle 1999; Miquelle *et al.* 2006). Multiple observations of similar-sized tracks in an area that approximates one home range are regarded as one individual. Female tigers with cubs are the most distinctive group due to track size and consistent group size, and, therefore, provide a check on estimating the 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 from covering many of the standard routes, and greatly restricted movements of ungulates and tigers (based on snow tracking and radio-collared tigers; unpublished 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, radio-collared individuals and track data).

Because the winter surveys were not instantaneous (data are collected over 3–4 months), some mortality and natality may have occurred 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 rates.

We believe this survey methodology is conservative in estimating population size because: (i) there is a probability of missing tracks of individuals, especially in remote sections of SABZ; and (ii) repeated reports of tracks in an area are conservatively interpreted; that is, 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 two or more. Although 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 SABZ (Soutyrina *et al.* 2013) generally support the interpretations of population structure and size reported here.

Because the size of the reserve fluctuated during the study period, we derived a density estimate as the *Total population count*/*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 1 year to the next, where

$$R_{real} = (N_i - N_{i-1}) / N_{i-1}, \text{ or } \lambda - 1, \text{ where } \lambda = (N_i / N_{i-1}) .$$

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 & 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.

Table 1 Results of tiger surveys in Sikhote–Alin Biosphere Zapovednik, 1966–2012 and tiger density derived from mean total numbers and size of the reserve

Year	Adult females	Adult males	Cubs	Undetermined sex–age	Number of litters	Total count	Zapovednik area (km ²)	Density (tigers/100km ²)
1966	2	0–1	1		1	3–4	3101.0	0.11
1967	2–3	1	3		2	6–7	2842.9	0.23
1968	3	1	3		1	7	2786.9	0.25
1969	3–4	1	4		1	8–9	2786.9	0.31
1970	3–4	1	4		2	8–9	2786.9	0.31
1971	3–4	1	2–3		0	6–8	2734.9	0.26
1972	3–4	1–2	2–3		1	7–9	2734.9	0.29
1973	4–5	2	5–6		2	10–13	2734.9	0.42
1974	4–5	2	4–5		1	10–12	3402.0	0.32
1975	4–5	2–3	5–6		1	10–14	3402.0	0.35
1976	4–5	2–3	4.5–6.5		1–2	10–15	3402.0	0.37
1977	5–6	2	7–8		2	14–16	3402.0	0.44
1978	5–7	2	8–9		2	15–18	3470.5	0.48
1979	4–6	2–3	6–8		0	12–17	3470.5	0.42
1980	5–7	2–3	8–10		4	15–20	3470.5	0.50
1981	6–8	2–3	8–10		1	16–21	3470.5	0.53
1982	5–6	2–3	9–11		2	16–20	3470.5	0.52
1983	5–6	3	6–8		2	14–17	3470.5	0.45
1984	7–9	3–4	10–11		3	18–24	3470.5	0.61
1985	7–9	3–4	11–12		4	21–25	3470.5	0.66
1986	6–8	3–4	12–13		4	21–25	3470.5	0.66
1987	6–8	4–5	15		4	22–28	3470.5	0.72
1988	7–9	3–4	12–14		2	19–26	3470.5	0.65
1989	7–9	4–5	10–11		2	21–25	3470.5	0.66
1990	8–10	3–4	8–9		4	20–24	3470.5	0.63
1991	7–9	3–4	12–13		4	21–26	3470.5	0.68
1992	6–8	3–5	18		4	27–31	3470.5	0.82
1993	7–10	3–5	15–16		6	24–31	3470.5	0.79
1994	10–12	6–8	7	2–5	4	25–32	3470.5	0.82
1995	12	5	12	4	8	33	3470.5	0.95
1996	8–11	6–7	14–15	1–2	7–8	29–35	3872.8	0.83
1997	8–12	6–8	7–8	5–10	4–5	26–38	3872.8	0.83
1998	8	7	10–11	4–5	5	29–31	3872.8	0.77
1999	7	6–9	8–9	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	5	6	2	27	3985.3	0.68
2007	11	11	8	8	3	38	3985.3	0.95
2008	12	7	7	8	4	34	3985.3	0.85
2009*	3	5	3	1	2	30	3985.3	0.75
2010	11	6	2	3		22	3985.3	0.50
2011	2	6	0	7	0	15	3985.3	0.38
2012	3	3	2	1	1	9	3985.3	0.23

*Record snowfalls prevented full survey. Estimate relied on snowtrack counts, camera traps, and radio-collared animals.

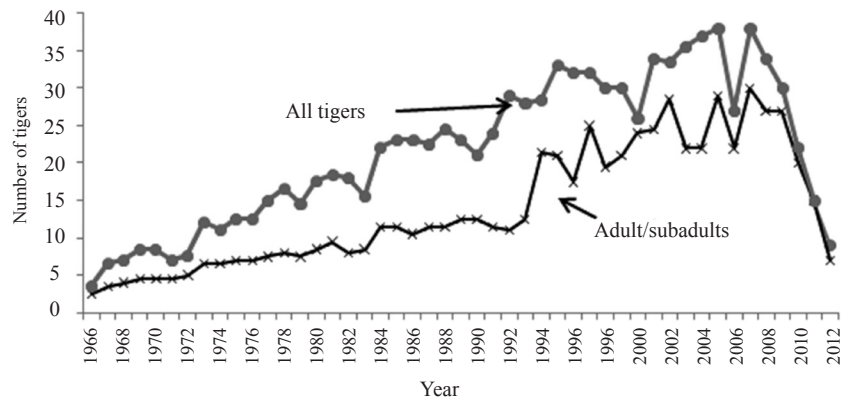


Figure 2 Yearly estimates of total population (in grey) and adult population (in black) of Amur tigers in Sikhote-Alin Biosphere Zapovednik, 1966–2012.

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: 4 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 5 periods to examine changes in sex ratio and reproduction rates using an analysis of variance. All means are reported with $\pm 95\%$ 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. Recol-

onization of the reserve began in 1966, when two 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 (Fig. 2). The total number of tigers (adults and cubs) peaked at 38 animals in 2005 and 2007 (Table 1, Fig. 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 km²). 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 the maximum density of adult tigers was also reached at 0.75/100 km² (Table 1).

Tiger numbers began to decline from a peak in 2007, but remained at or above 30 until 2010, when a dramatic drop occurred, and continued through 2012, when tigers reached their lowest point (9 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 (Fig. 3). While this smoothing function appears to do a good job of dealing with yearly fluctuations in tiger numbers during the growth phase, it inaccurately 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 $4.6\% \pm 7.0\%$, with the large confidence interval an indication of the great variation in growth rates

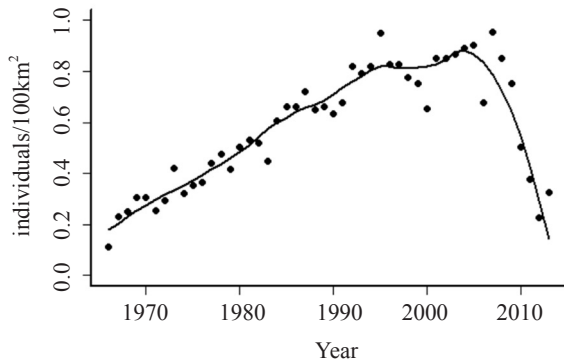


Figure 3 The smoothed loess regression represents growth of the tiger population (based on density estimates) from 1966 to 2012 at Sikhote-Alin Biosphere Zapovednik.

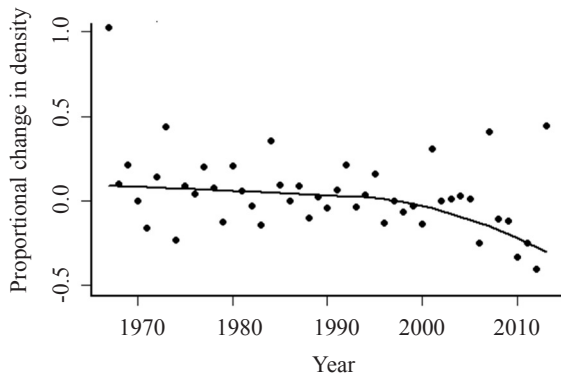


Figure 4 Proportional change in growth (R_{real}) of the Amur tiger population in Sikhote-Alin Biosphere Zapovednik from 1966 through 2012.

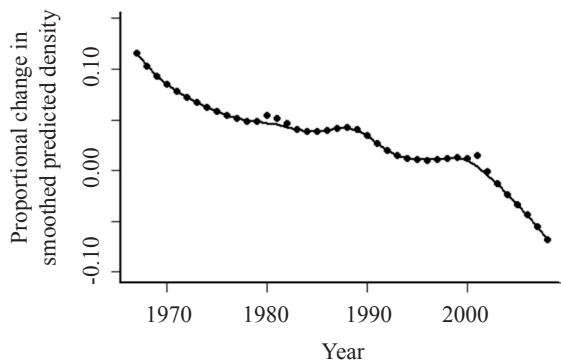


Figure 5 Estimated values of proportional change (R_{real}) in tiger numbers based on smoothed values of density (from Fig. 3) of Amur tigers in Sikhote-Alin Biosphere Zapovednik, 1966–2012.

over time. Although the population appeared to increase in a linear manner (Fig. 3), the proportional change in tiger numbers (R_{real}) varied greatly (Fig. 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. Using the loess smoothing regression applied to the proportional change in tiger numbers (R_{real}) from Fig. 4 (Fig. 5) provides a much clearer picture. Growth rates were high in the early years of this study (6–10%) but dropped below 6% within 9 years, and continued to drop until they reached 1% in the early 1990s.

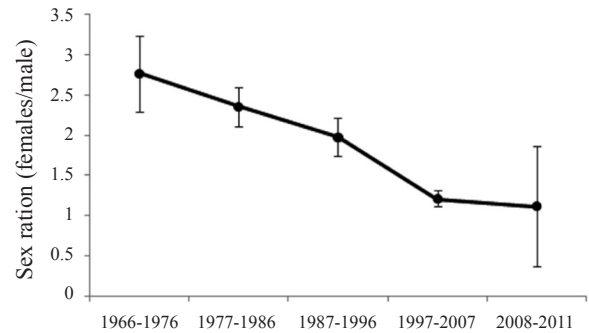


Figure 6 Sex ratio (adult females per 1 adult male) of Amur tigers over 5 periods in Sikhote-Alin Biosphere Zapovednik, 1966–2012.

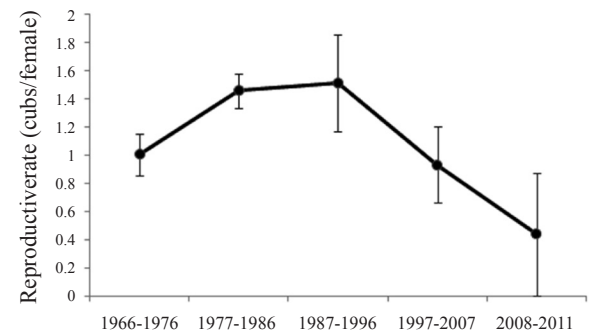


Figure 7 Reproductive rate (cubs/female/year) of tigers in Sikhote-Alin Biosphere Zapovednik for 5 periods of observation, 1966–2012.

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†	Chitwan Nepal‡	Ramtham-bore India§	Pench India§	Panna India¶
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: †Kerley *et al.* (2003), ‡Smith *et al.* (1991), §Singh *et al.* (2013, 2014) and ¶Chundawat *et al.* (2002).

Sex ratio and reproduction parameters

The sex ratio of the SABZ tiger population averaged 1.97 ± 0.23 females/male, and 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 5 observation periods (ANOVA $F_{4,42} = 16.01$, $P < 0.0001$) (Fig. 6).

Reproductive rates (Fig. 7) also varied significantly by period ($F_{4,42} = 4.61$, $P = 0.0003$), with a peak within the two periods from 1977 to 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 (Fig. 2) reflects the higher reproduction rates during this period ($F_{4,41} = 21.0$, $P < 0.0001$). 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 the size of the Zapovednik was cut to 1000 km². Matyushkin *et al.* (1981) plot-

ted the frequency of tracks within SABZ from 1957 through 1978 and reported that even though the size of the Zapovednik was restored to 3101 km² in 1960, the population of tigers continued to collapse and tracks completely disappeared from the reserve for 3 years, 1963–1965 (see Smirnov & Miquelle 1999). The localized extinction of this population was attributed to illegal hunting (new logging roads into former protected areas in the 1950s eliminated de facto protection) and continued capture of cubs. Despite supposedly tighter controls, in the winters of 1962–1963 and 1963–1964, 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 emigration into the reserve an additional likely source of growth. Therefore, the observed rate of increase for the SABZ population during that initial phase (>10%) is probably close to the maximum rate of increase that might be expected; that is, 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% (Fig. 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 (Fig. 5). However, 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.

However, 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-1970s, 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 radio-collared sub-adult 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, 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. Although there is variation in reproduction parameters in the Indian subcontinent and

there are 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 *et al.* 2015), but similar data is absent from the Indian subcontinent. Hence, while comparison of mortality rates is not possible, available evidence suggests that 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 and 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 the 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 (Aryal *et al.* 2015). 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 the estimate in Karanth *et al.* (2006) 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.* (2015) and Robinson *et al.* (2015). 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 (Miquelle *et al.*, 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 virus (CDV), 3 cubs died because their mother contracted CDV and were abandoned; two radio-collared tigers died of unknown causes but CDV 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 (Fig. 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.* 2015), 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 SABZ, 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; Abramov 1960; Yudakov & Nikalaev 1972; Pikunov *et al.* 1983; Smith & McDougal 1991). 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 fe-

males may have been common because 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 5 subadult males we have monitored during the later phases of this dataset (Goodrich *et al.* 2008), 4 dispersed outside SABZ, suggesting that most subadult males were still dispersing far from natal home ranges.

Alternatively, the shift in the 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 SABZ (Goodrich *et al.* 2010; Hojnowski *et al.* 2013) may break down, at least for male tigers, as has been documented further south in Russia (Hernandez-Blanco *et al.* 2015).

Reproduction rates 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 2 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 and 0.32 per 100 km², 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 & Miquelle 1999) reported a much higher density (0.62/100 km²), 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 km².

In 2007, the tiger density in Sikhote-Alin was as great as that found in Lazovskii Zapovednik (0.7–1.4 animals/100 km²), 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; 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.* 2015) 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 Fig. 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 undertaken 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. Although a 10% growth rate would double numbers in less than 9 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. First, 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. Second, 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. Third, while growth is slow, decline of tiger populations can be rapid. Fourth, 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. Finally, achieving the “2×T” goal of the Global Tiger Initiative would require high growth rates across multiple tiger landscapes simultaneously, and is, therefore, extremely unlikely, but a noble goal worth striving for.

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