Population dynamics of the Amur tiger in Sikhote-Alin Zapovednik, Russia

Evgeny N. Smirnov and Dale G. Miquelle

Introduction

Very little is known about population dynamics of tigers. Nearly all information comes from one population of Indian tigers in Royal Chitwan National Park, Nepal (McDougal 1977; Sunquist 1981; Smith & McDougal 1991), or from the study of captive individuals (Sadleir 1966; Kleiman 1974; Seal *et al.* 1987b). Information on population growth rates is largely lacking.

Despite the lack of knowledge, such information is important to conservation efforts for this endangered species. As the tiger is presently threatened with extinction due to poaching throughout much of its range (Jackson 1993b; S. R. Galster & K. V. Eliot this volume), estimates of its reproductive potential are critical to establishing the extent of illegal harvesting that can be sustained (e.g. Kenney *et al.* 1995). Little information exists to make such assessments.

Information on the distribution and status of Amur, or Siberian, tigers in Sikhote-Alin has been collected since creation of the protected area in 1935 (Matyushkin *et al.* 1981). Here we present estimates of the size and structure of that population based on a long-term monitoring programme that has been conducted in Sikhote-Alin State Biosphere Zapovednik since 1963. The purpose of this study was to use existing information to estimate observed population growth rate and reproductive parameters and to consider some of the implications for tiger conservation.

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Study area and methods

Lands designated as 'Zapovedniks' receive the highest level of nature protection in Russia; human access is limited to forest guards and scientists. Sikhote-Alin State Biosphere Zapovednik is located close to the northern border of Primorski Krai (Province), with nearly all its territory situated within Terney Raion (District) (Fig. 5.1). Size of the Zapovednik has changed dramatically over time, reaching 1 157 000 ha when borders were delineated in 1938. In 1951 the Zapovednik was reduced to a low of 99 000 ha; presently it is approximately 400 000 ha. Portions of Sikhote-Alin Zapovednik border the Sea of Japan, but its central feature is the Sikhote-Alin Mountains, a low range (most peaks are below 1200 m) that parallels the Sea of Japan and bisects Primorski and Khabarovski Krais. Sikhote-Alin Zapovednik is situated close to the centre of remaining Amur tiger population (Matyushkin *et al.* 1996) and, with Lazovski Zapovednik, probably represents some of the best conditions remaining for Amur tigers due to its large size and the protection afforded to both tiger and prey populations.

Yearly surveys to estimate tiger numbers in Sikhote-Alin Zapovednik and adjacent lands

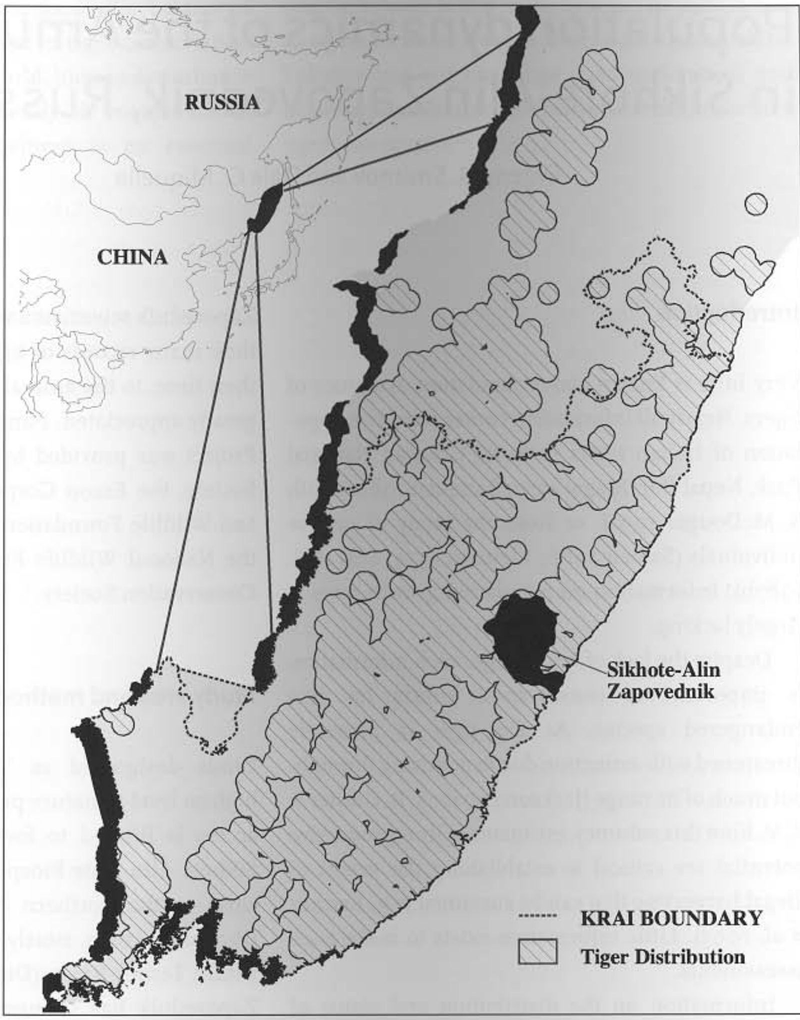

FIGURE 5.1
Location of Sikhote-Alin Biosphere State Zapovednik in Primorski Krai, Russian Far East. Scale: 1cm = 70km

together covered a total area of approximately 500 000 ha. Information on tiger abundance has been collected since 1963, but since evidence of tigers was not found during the first three years, estimates are based on data collected during the 28 years from 1966 to 1993 inclusively.

Methods for estimating tiger numbers, sex and age structure are based on two types of information. Since 1971, annual surveys have been conducted by 20–28 people along 300–400 km of permanently established transects. These surveys are conducted one to three times per year after recent snowfall. Location, number and size of all tiger tracks are recorded. Secondly, forest guards located at permanent stations throughout Sikhote-Alin Zapovednik spend extensive time patrolling and, together with all scientists working in Sikhote-Alin Zapovednik (collectively averaging approximately 50 individuals per year), they record all observations of tiger tracks. All records from each winter count and reports are tabulated chronologically and by area. Nearly all information comes from tabulation of tracks in snow, the season of snow cover usually lasting approximately three to four months (December–March).

Tracks of tigers are placed into four sex and age categories based on the width of the pad on the front paw (Abramov 1961; Matyushkin & Yudakov 1974; Yudakov & Nikolaev 1987; Matyushkin *et al.* 1996): tigers with pad widths equal to or greater than 10.5 cm are considered adult males; pad widths of 8.5–10.5 cm are considered adult females; pad widths of 7–8.5 cm are defined as subadults (yearlings and some two-year-olds fall into this group); and pad widths less than 7 cm are defined as first-year cubs. The confounding problem with this method of identification comes with young males: the track size of subadult males overlaps with that of females, but by the time most subadult males disperse, their track size is already greater than that of adult females. Prior to dispersal, most subadult males are identifiable because they are associated with a family unit. The subadult classification is most poorly defined because it includes some yearlings still in association with a family unit, as well as some yearlings and two-year-olds that have dispersed. Despite these problems, definition of these broad categories has been verified with measurements of freshly killed specimens (Yudakov & Nikolaev 1987), and with 19 individuals captured within Sikhote-Alin Zapovednik for the Siberian Tiger Ecology Project (Smirnov *et al.* 1997).

Records of all tracks are plotted, and population size and structure are derived by estimating the number of individuals in the study area, overlapping and adjacent individuals being distinguished by the size of their tracks and their temporal-spatial distribution. Given that home range estimates of resident females and males exist (Yudakov & Nikolaev 1987; Salkina 1993; D. G. Miquelle *et al.*, unpubl. data), it is possible to estimate the number of duplicate tracks of one individual based on

Amur tigers live at such low density that 'camera-trapping' is rarely successful. This rare photograph was taken with a home-made camera-trap triggered by a trip wire in Lazovsky Zapovednik in 1992.

size and temporal-spatial distribution. Repeated observations of similar-sized tracks in a limited region are considered one individual. Females with cubs are the most distinctive group due to track size, consistent group size and reduced home range size (Smith 1984; D. G. Miquelle *et al.* unpubl. data), and therefore provide a check on estimating the frequency of repeated track sightings of specific individuals.

We believe the procedure is conservative in estimating population size because: (1) there is a probability of missing tracks of individuals, especially in remote sections of Sikhote-Alin Zapovednik; 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 two 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, though we cannot assess how well they reflect true population size. Initial estimates based on radio-collared tigers in Sikhote-Alin Zapovednik support the interpretations of population structure and size reported here, and also suggest that the procedure provides a conservative estimate of population size (Smirnov & Miquelle 1995).

Population density is estimated for the entire study area (500 000 ha) for total population size, and for the adult population only. The adult population includes all individuals except young still associated with a family unit. The observed exponential rate of increase, r, is calculated by regression analysis (Caughley 1977) for the total population count, and for adults only. Slopes were tested to determine if growth rates varied significantly from each other, and from zero (Zar 1984). Because the count is not instantaneous, some mortality and natality may occur during the count period, introducing an unknown amount of error to the method. However, most births occur outside the period when snow is on the ground (Seal *et al.* 1987b; E. N. Smirnov *et al.* unpubl. data), and the bias associated with mortality should have been generally consistent throughout the period of study, thereby not biasing estimates of growth rate.

Tracks of females with and without cubs provided estimates of the following reproductive parameters: litter size, percentage of adult females with cubs and reproduction rate. This methodology, similar to that used by Smith & McDougal (1991), does not estimate litter size at birth; it provides a conservative estimate of litter size because young are generally not detected before two to three months of age, when cubs become mobile and follow mothers to kills (Smith 1984; D. G. Miquelle *et al.* unpubl. data). Many litters are considerably older before they are detected in winter counts. Therefore, some mortality no doubt occurs before litters are registered. The reproduction rate was estimated as number of cubs per adult female per year, averaged over years. This estimate is slightly different than that reported elsewhere for large carnivores (Craighead *et al.* 1974; Wielgus & Bunnell 1994) where reproduction rate equals the mean litter size divided by mean birth interval. We use this calculation because mean birth interval is poorly known for Amur tigers.

The study period was divided into three approximately equal periods of 9–10 years: Period 1=1966–1975; Period 2=1976–1984; and Period 3=1985–1993. Changes in three reproductive parameters, i.e. reproduction rate, percentage of females with cubs/year and litter size, were assessed over these three time periods using analysis of variance with protected least significant difference (LSD) tests (SAS 1985). All means are reported ± standard deviations.

Results

Population estimates are based on 5203 reports of tracks or visual sightings from 1966 to 1993. The number of reports ranged from 19 in 1966 to 339 in 1985 ($\bar{x}$=185.8±88.3).

Table 5.1. *Estimates of size, sex and age structure of the Amur tiger population in Sikhote-Alin State Biosphere Zapovednik, 1966–93*

Year	Adult females	Adult males	Subadults	<1-year-old cubs	No. of litters	Total count
1966	2	0–1	0	1	1	3–4
1967	2–3	1	1	2	2	6–7
1968	3	1	2	1	1	7
1969	3–4	1	2	2	1	8–9
1970	3–4	1	2	2	2	8–9
1971	3–4	1	2–3	0	0	6–8
1972	3–4	1–2	1–2	1	1	6–9
1973	4–5	2	2–3	3	2	11–13
1974	4–5	2	3–4	1	1	10–12
1975	4–5	2–3	4–5	1	1	11–14
1976	4–5	2–3	3–5	1–2	1–2	10–15
1977	5–6	2	2–3	5	2	14–16
1978	5–7	2	6–7	2	2	15–18
1979	4–6	2–3	6–8	0	0	12–17
1980	5–7	2–3	2–4	6	4	15–20
1981	6–8	2–3	6–8	2	1	16–21
1982	5–6	2–3	4–6	5	2	16–20
1983	5–6	3	2–4	4	2	14–17
1984	7–9	3–4	5–6	5	3	20–24
1985	7–9	3–4	5–6	6	4	21–25
1986	6–8	3–4	5–6	7	4	21–25
1987	6–8	4–5	5	10	4	25–28
1988	7–9	3–4	8–10	4	2	22–27
1989	7–9	4–5	5–6	5	2	21–25
1990	8–10	3–4	4–5	4	4	19–23
1991	7–9	3–4	4–5	8	4	22–26
1992	6–8	3–5	10	8	4	27–31
1993	7–10	3–5	5–6	10	6	25–31

Between 1963 and 1965 there was no evidence of tigers consistently residing within the study area. Although it is likely that animals were establishing home ranges during this period, the first evidence of resident tigers during the 1960s came in 1966, when two females, one with a litter of one, were reported (Table 5.1). Total population size increased, with some fluctuations, during the entire 28 years of study (Fig. 5.2). However, the adult population appeared to stabilise beginning in 1983, when the adult female and male counts became fairly consistent for the next 10 years (Fig. 5.2 and Table 5.1).

The maximum estimated density of the Sikhote-Alin Zapovednik tiger population was reported in 1992 and 1993, when the total population density was 0.62/100 km². The maximum adult population estimate, reached in 1993, was 0.3/100 km². The sex ratio of the population averaged 2.4 females/male (SD=0.54, *n*=28).

For the 28-year period, the observed rate of increase for the entire population was 0.06 (Fig. 5.3). The rate of increase appeared to be slightly higher during the 1970s and early 1980s and then dropped slightly (Fig. 5.3). From 1966 to 1984 the observed rate of increase of the adult population (r=0.064) was not significantly different from that of the total population (t=0.956, $P > 0.05$). However, from 1985 to 1993, the total population continued

Table 5.2. *Reproduction rate (cubs/adult female per year), percentage of females with cubs, and litter size of Amur tigers in Sikhote-Alin State Biosphere Zapovednik, Russian Far East, during three time periods between 1966 and 1993*

	Reproductive rate			Percentage of females with cubs			Litter size		
Period	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
1966–1975	10	0.39[a]	0.27	10	37	22	12	1.2[a]	0.39
1976–1984	9	0.57[b]	0.35	9	31	18	17	1.8[b]	0.81
1985–1993	9	0.90[b]	0.33	9	48	15	34	1.9[b]	0.92
Overall value	28	0.61	0.37	28	39	20	63	1.7	0.85

Periods with different letters are significantly different (P <0.05)

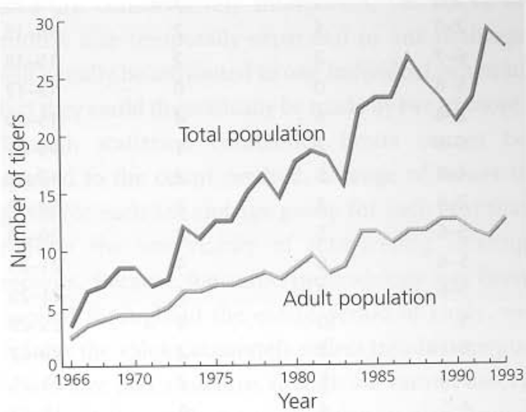

FIGURE 5.2
Size of Amur tiger population (total population and adult component) in Sikhote-Alin Biosphere State Zapovednik from 1966 to 1993.

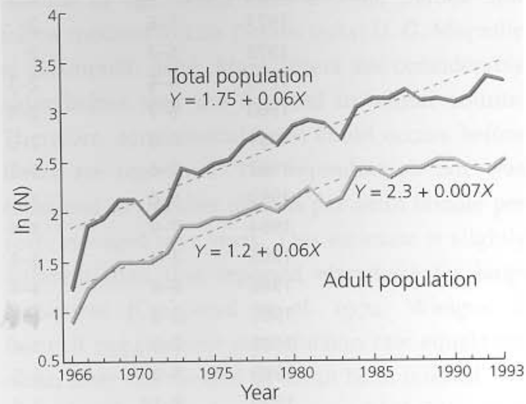

FIGURE 5.3
Population size (natural logarithm of n) and regression equations defining exponential rate of increase for total population, and adult population in Sikhote-Alin State Biosphere Zapovednik, Russian Far East, 1966–1993.

to increase (Fig. 5.2), while the observed rate of growth of the adult population (r=0.007) was not significantly different from 0 (F=1.45, P=0.263).

The increasing divergence in total population and adult population size (Fig. 5.2) appears to be due not only to a stabilisation in the adult population, but to an increase in the reproductive rate. The proportion of females with cubs over the entire study period averaged 38.8% (SD=19.6). However, the reproduction rate increased over the three time periods (F=6.13, P=0.007) (Table 5.2), with a significant difference between Period 1 (1966–75) and the two later periods (Table 5.2).

The increase in reproduction rate (cubs per adult female per year) was related to an increase in litter size (Tables 5.2 and 5.3). During Period 1, most reported litters (83%) consisted of a single cub, whereas during Period 3 more than 50% of the litters had two or more cubs and 30% of the litters had three or more (Table 5.3). Litter size during Period 1 was significantly lower than during the other two periods (F=3.31, P<0.05) (Table 5.2).

It is not clear if the increase in reproduction rate

Table 5.3. *Distribution of litter sizes reported for Amur tigers in Sikhote-Alin State Biosphere Zapovednik, Russian Far East, for three time periods between 1966 and 1993*

Period	Litter size				Total
	1	2	3	4	
1966–1975	10	2	0	0	12
1976–1984	7	6	4	0	17
1985–1993	16	8	9	1	34
Total	33	16	13	1	63

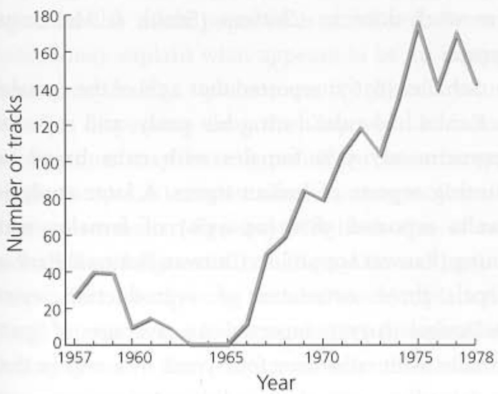

FIGURE 5.4
Frequency of tracks located within Sikhote-Alin Zapovednik, 1957–1978 (from Matyushkin *et al.* 1981).

was also related to an increase in the percentage of females with cubs. Although there were no significant changes throughout the period of study (F=1.91, P=0.16), the percentage of females with cubs in Period 3 (48%) was considerably higher than in either of the earlier periods (Table 5.2).

Discussion

In 1939–40 Kaplanov (1948) estimated that there were 10–12 tigers within Sikhote-Alin Zapovednik, but that these animals were confined to some 30 000 ha of the Zapovednik. During this period the size of the Amur tiger population apparently reached its lowest level; Kaplanov (1948) suggested that the isolated population within the Zapovednik may have represented one-half of the total population remaining in the Russian Far East. With the outlawing of hunting (in 1947), and tighter controls on capture of cubs (1956), the overall population in the Russian Far East began an expansion phase that continued into the 1980s (Matyushkin *et al.* 1996). However, locally, the protection provided by Sikhote-Alin Zapovednik was severely dampened in 1951 when size of the Zapovednik was cut to 99 000 ha.

Matyushkin *et al.* (1981) plotted the frequency of tracks within Sikhote-Alin Zapovednik from 1957 through 1978 (Fig. 5.4). Even though the size of the Zapovednik was restored to 310 100 ha in 1960, the population of tigers continued to collapse. The localised 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. In the winters of 1962–63 and 1963–64, 14 cubs were captured within former Zapovednik territory. Attempts to capture cubs often resulted in the death of the female. Apparently, both the reproductive and recruitment components of this population were simultaneously eliminated by the mid-1960s.

The growth of the Sikhote-Alin Zapovednik population since 1966 therefore apparently represents a colonisation episode. Poaching of both prey species and tigers was rare throughout 1991 due to tight control of firearms, regular patrolling of the Zapovednik and no economic incentives (access to the international market for tiger skins and bones was virtually non-existent due to the closure of borders). Given these conditions, the colonisation episode occurred in what was probably high-quality habitat for Amur tigers with minimal human impact. Therefore, the observed rate of increase in the Sikhote-Alin Zapovednik population is probably close to the maximum rate of increase that might be expected during a colonisation phase. However, this estimate is not equal to the intrinsic rate of increase, i.e. the exponential rate at which a population grows when no resource is limited (Caughley 1977) for two reasons: (1) the age distribution was not stable during this period, a necessary assumption for estimating intrinsic rate of increase (Caughley 1977); and (2) dispersal probably played an important role in reducing the rate of growth (see later). Nonetheless, this estimate is valuable because it provides an index of how quickly Amur tiger populations could grow in newly colonised areas with healthy prey populations. Tigers have been extirpated from much of their former range and, if reintroduction becomes a possibility, this estimate provides an indication of potential population growth rate.

These data represent the first estimates of population growth rates that exist for the tiger, so it is impossible to make comparisons with other subspecies or other studies. Population growth was not as rapid as might be expected, given the nearly optimal conditions that existed during much of the study period. The population grew at a fairly consistent rate over 18 years, and did not mimic the 'classic' sigmoidal growth curve. Dispersal may have played an important role in reducing population growth rate. Matyushkin *et al.* (1981) reported that the region to the north of Sikhote-Alin Zapovednik was still uncolonised in the mid-1970s, and Pikunov (1988) reported the region to be sparsely populated with tigers in 1985. Only recently is there evidence to suggest that tigers have colonised the entire region of Terney Raion (Smirnov & Miquelle 1995). Therefore, areas outside the Zapovednik may have acted as dispersal sinks. Given the present level of poaching activity (S. R. Galster & K. V. Eliot this volume), regions adjacent to the Zapovednik may continue to act as sinks, especially since dispersing individuals may be especially vulnerable to poaching activity (Garshelis 1994). It remains to be seen whether population size within Sikhote-Alin Zapovednik stabilises in what appears to be a saturated population of adult animals. Presently, it appears that the colonisation phase lasted approximately 19 years, with the adult population approaching a threshold around 1984.

Estimates of population and reproductive parameters vary only slightly in comparison to information on other subspecies. For Indian tigers in Kanha Tiger Reserve in India, Schaller (1967) reported a sex ratio (females:males) in the adult population of 4:1 and 5:1. Smith and McDougal (1991) reported a sex ratio of 2.25:1 in Royal Chitwan National Park, Nepal. The sex ratio of the entire Amur tiger population can be estimated for at least four time periods from census data: in 1956–57 it was estimated at 1:1 (Abramov 1960); in 1959 at 1.3:1 (Abramov 1965); in 1969–70 at 1.7:1 (Yudakov & Nikolaev 1970), and in 1978–79 at 1.5:1 (Pikunov *et al.* 1983). All these estimates suggest a lower sex ratio than the 2.4:1 found in Sikhote-Alin Zapovednik, which is nearly identical to the intensive work done in Chitwan (Smith & McDougal 1991).

Schaller (1967) reported that 25% of the females in Kanha had cubs during his study, and reported approximately 33% females with cubs based on hunting reports of Indian tigers. A later study in Kanha reported 38% (25–43%) of females with young (Panwar 1979b). In Chitwan National Park in Nepal, three estimates of reproduction exist. McDougal (1977) reported an average of 50% females with cubs over four years in a region that contained two to three adult resident tigresses (calculated from data, p. 96), Sunquist (1981) reported 75% of resident females with young in 1976, and Smith (1978) reported 87% in 1978. Additionally, McDougal (1977) questions the accuracy of Schaller's figures, and suggests the true value to be much higher. All estimates from Chitwan are based on resident females, a social status that could not be exactly determined by our counting techniques (or those of Schaller). Abramov (1977) estimated the percentage of females with cubs as 20–25% for the Primorye population, a slightly lower estimate than the 38% we report for Sikhote-Alin Zapovednik. Differences in counting techniques make it difficult to determine whether reproduction rates of Amur tigers are actually lower than those of Indian tigers in the wild, or whether the apparent difference is a methodological artefact.

Sadleir (1966) reported that the average size of 79 litters raised in zoos was 2.8. The average size of

49 litters in Royal Chitwan National Park, Nepal was 2.8 (Smith & McDougal 1991). Using a technique similar to that of Smith and McDougal (1991), the average litter size in Sikhote-Alin, 1.7, is substantially less than that of the Indian tiger in the wild.

Our observations of reproductive parameters are counterintuitive to what would be expected if density-dependent effects became important as the tiger population approached carrying capacity. Reproductive rates and/or survival rates (especially of young) should have decreased as the region became saturated (e.g. Beier 1993; Garshelis 1994). However, both litter size and reproductive rate increased through the period of study, and young actually became a larger percentage of the population as the adult population stabilised. Several factors may explain what appears to be an inverse density-dependent phenomenon. First, young females dispersing into the Zapovednik during colonisation may have experienced lower reproductive output, a trait common to young mothers in many mammalian species (first litter size of two radio-collared tigresses in Sikhote-Alin was one). A preponderance of young females would explain the small litter size and low reproductive rate observed during Period 1. Secondly, as already noted, during the earlier stages of colonisation dispersal may have played an important role dampening the population growth rate, and reducing the percentage of subadults in the population. However, as adjacent regions became colonised, a greater percentage of subadults may have remained within the study area, since adjacent areas no longer provided the advantage of no competition for space. The fact that subadults made up a smaller percentage of the population in Period 1 (41%) compared to Periods 2 and 3 (58 and 53% respectively) supports this hypothesis. The data, as presented here (Table 5.1), do not allow assessment of whether the subadult male segment of the population (that most likely to disperse long distances) increased disproportionately, which would substantiate the hypothesis that fewer subadults were dispersing. However unlikely, available information does not rule out the possibility that survival of subadults did actually increase in an inverse density-dependent manner.

We believe that the existent population density may well reflect carrying capacity for this region, given the present density of ungulates. The same prediction has already been made for this population at lower densities. Between 1972 and 1977 Matyushkin *et al.* (1980) estimated the tiger density in Sikhote-Alin Zapovednik to be 0.13–0.32/100 km^2, and stated that the population probably represented a maximum for the conifer-broadleaf forests of central Sikhote-Alin mountains. However, densities have increased substantially since that time. Although not reported here, the density of tigers does vary among different regions within Sikhote-Alin Zapovednik. Highest densities occur along the coast of the Sea of Japan, and may reach 0.8/100 km^2. Lazovsky Zapovednik, some 300 km to the south, is considered better tiger habitat due to higher prey densities (Matyushkin *et al.* 1980). Zhivotchenko (1981) estimated tiger density at 1.4/100 km^2 between 1973 and 1979. Matyushkin *et al.* (1980) reported tiger density in the Lazo region as 0.6–0.9/100 km^2 for 1975, and more recently Salkina (1993) reported a density of 0.7/100 km^2 for 1991, with maximum density in one area reaching 1.03/100 km^2. Despite the claim that habitat quality is better there, the differences in tiger density appear relatively small. Both sets of estimates, based on populations largely protected within Zapovedniks, likely represent the highest densities reached by Amur tigers in the existing range.

Despite the fact that these values may represent maximums for the Amur tiger, they are dramatically lower than that reported for other subspecies. While in some degraded habitats in Asia population densities are as low as 1.0/100 km^2 (Rabinowitz 1993), tiger densities can reach as high as 11.6 individuals/100 km^2 (Karanth 1991). Low densities of Amur tigers, even in quality habitat, coupled with low reproductive potential in comparison to other subspecies, demonstrate the problems of conservation for this subspecies. Very large tracts of land must be preserved to ensure survival of a viable population, and population responses to poaching or other sources of mortality may not be as rapid as in regions to the south. Sikhote-Alin Zapovednik, the largest protected reserve in remaining Amur tiger habitat, contains only 10–15 adults at its present high density. It is unlikely that more space for resident adults exists (see D. G Miquelle *et al.* this volume, Chapter 19), or that the size of the Zapovednik can be increased sufficiently to ensure population viability. The key to ensuring survival of the Amur tiger will be the development of a connected network of protected and managed lands that will provide for a minimum population, and management of additional lands through a zoning process that will allow for human uses of the landscape that are compatible with tiger conservation (D. G. Miquelle *et al.* this volume, Chapter 19). Conservation of this subspecies will therefore depend on developing a strategy that not only increases the amount of protected lands, but also seeks ways to mitigate the impact of resource extraction on non-protected lands.