Effects of Roads and Human Disturbance on Amur Tigers

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Abstract: *Understanding the effects of human disturbance on endangered wildlife populations is critical to their conservation. We examined the effects of roads and human disturbance on the survivorship and foraging efficiency of Amur tigers (*Panthera tigris altaica*) on and near Sikhote-Alin State Biosphere Zapovednik, Primorye Krai (province), Russia. To evaluate the effects of roads, we estimated survivorship of radiocollared tigers and their cubs living in three types of areas: (1) areas with primary roads, (2) areas containing secondary roads, and (3) areas with minimal or no road access. We classified a tiger into one of these three treatments based on which types of roads bisected their 50% minimum convex polygon home ranges. Over a 9-year period (1991–2000), adult female survival was greatest ($\chi^2 = 12.2$, df = 2, $p = 0.002$) for radiocollared tigers in roadless areas. All adult female tigers in roadless areas survived their tenure in those locations ($n = 2$), whereas all died or disappeared prematurely from areas with primary roads ($n = 6$). Cub survival was lower in areas with primary and secondary roads than in roadless areas ($\chi^2 = 10.9$, df = 1, $p < 0.009$). We evaluated the effects of human disturbance at kill sites by examining 86 kills made by 15 tigers determining whether human disturbance had occurred at the kill site, and examining prey carcasses after tigers left, to estimate the percent meat eaten and whether the tiger abandoned the kill following human disturbance. Tigers undisturbed at kills consumed more meat ($Z = 3.71$, $p = 0.0002$) from each kill than disturbed tigers did. Undisturbed tigers also spent more time at each kill site than disturbed tigers did ($Z = 2.3$; $p = 0.02$). Abandonment of kills occurred in 63% of 24 instances when tigers were disturbed by people. Because roads decrease the survivorship and reproductive success of tigers, we recommend that in habitats managed for tigers, construction of new roads should be prohibited wherever possible and access to secondary roads (e.g., logging roads) should be reduced or prevented wherever possible. Protected areas seem to cease functioning as source populations where road access exists, and unprotected areas—the majority of Amur tiger range—cannot sustain stable populations with the increasing threat of human access to tiger habitat.*

Efectos de Caminos y Perturbación Humana sobre Tigres Amur

Resumen: *Entender los efectos de la perturbación humana sobre poblaciones de vida silvestre en peligro es crítico para su conservación. Examinamos los efectos de caminos y perturbación humana sobre la supervivencia y eficiencia de forrajeo de tigres Amur (*Panthera tigris altaica*) en y cerca de Biosfera Estatal Zapovednik Sikhote-Alin, Primorye Krai (provincia), Rusia. Para evaluar los efectos de los caminos, estimamos la supervivencia de tigres con radio-collares y sus crías en áreas de tres tipos: 1) áreas con caminos primarios, 2) áreas con caminos secundarios y 3) áreas con mínimo o sin acceso de caminos. Clasificamos un tigre en uno de estos tres tratamientos con base en cuales tipos de caminos dividen el 50 % mínimo del polígono convexo de sus rangos de hogar. En un período de 9 años (1991–2000), la supervivencia de hembras adultas fue mayor ($\chi^2 = 12.2$, g.l. = 2, $p = 0.002$) en tigres con radio-collar en áreas sin caminos. Todas*

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*las hembras adultas en áreas sin caminos sobrevivieron su dominio en esas localidades (*n *= 2), mientras que todas murieron o desaparecieron prematuramente en las áreas con caminos primarios (*n *= 6). La supervivencia de crías fue menor en áreas con caminos primarios y secundarios que en áreas sin caminos (χ^2 = 10.9, g.l. = 1,* p *< 0.009). Evaluamos los efectos de la perturbación humana en sitios de depredación mediante el examen de 86 muertes causadas por 15 tigres, determinando si había ocurrido perturbación humana en el sitio, y mediante el examen de restos de las presas después de que se alejaron los tigres, para estimar el porcentaje de carne consumida y si el tigre abandonó su presa después de una perturbación humana. Los tigres no perturbados consumieron más carne (Z = 3.71,* p *= 0.0002) de cada presa que los tigres perturbados. Tigres no perturbados pasaron más tiempo con su presa que tigres perturbados (Z = 2.3,* p *= 0.02). El abandono de presas ocurrió en 63 % de 24 eventos cuando los tigres fueron perturbados por humanos. Debido a que los caminos reducen la supervivencia y el éxito reproductivo de los tigres, recomendamos que en los hábitats bajo manejo para tigres, se debe prohibir la construcción de caminos donde sea posible y se debe reducir o prevenir el acceso a caminos secundarios (e. g. caminos madereros) donde sea posible. Las áreas protegidas dejan de funcionar como poblaciones fuente donde existe acceso a caminos, y las áreas no protegidas (la mayor parte del rango de tigre Amur) no pueden sostener poblaciones estables con la incremento en la amenaza del acceso humano al hábitat de los tigres.*

Introduction

Understanding the effects of human disturbance is critical for effective management and conservation of endangered species. Roads can have a major effect on large-carnivore mortality directly via vehicle collisions, overhunting, and poaching, and indirectly by providing greater hunting access that can result in reduced prey availability (e.g., Brody 1984; Thiel 1985; Mattson et al. 1987; McLellan & Shackleton 1988; Mech et al. 1988; Noss et al. 1996). Human presence in wildlands can disturb animals, causing them to unnecessarily expend energy avoiding people, thereby potentially reducing reproductive success (e.g., Manville 1983; van Dyke et al. 1986; Goodrich & Berger 1994; Primm 1996) or increasing the likelihood of fatal encounters with humans (Kasworm & Manley 1990; Saberwal et al. 1994; Khramtsov, 1995; Mattson et al. 1996).

Tigers (*Panthera tigris*) are endangered throughout their range. Three subspecies have become extinct since the 1950s due to human disturbances, including habitat loss, population fragmentation, and poaching (Seidensticker 1986; Mills & Jackson 1994; Nowell & Jackson 1996; William & Rabinowitz 1996). Although fewer than 400 adult individuals remain in the wild (Matyushkin et al. 1996), the Amur (or Siberian) tiger (*Pantherea tigris altaica*) may have a greater chance of survival than other subspecies because it inhabits a large block of relatively unfragmented and undisturbed habitat in the Russian Far East with low human population density (Miquelle et al. 1993, 1999; Matyushkin et al. 1996). But with the breakup of the Soviet Union and subsequent changes in the political and economic structure of Russia, human disturbances within the Amur tiger's range are increasing (Smirnov & Miquelle 1999; Miquelle et al. 1999).

Although protected areas should adequately safeguard tiger habitat within their boundaries, human activities that affect tigers still may occur in these areas (Smirnov & Miquelle 1999). Tourism in protected areas and consumptive activities (e.g., hunting, logging, and collection of nontimber forest products) and nonconsumptive activities (e.g., recreation, tourism, filming, and photography) in unprotected areas are increasing in Amur tiger habitat as road densities increase, car ownership increases, and demand for forest products continues during a period of economic instability. Although the direct effects of human activities such as habitat loss and poaching are readily discernible, the effects of other human activities, such as those discussed above, are subtle and more difficult to document.

Successful conservation of Amur tigers must include a proactive approach to managing protected areas as source populations (Matyushkin 1996; Smirnov & Miquelle 1999; Miquelle et al. 1999) and reducing human effects in both protected and unprotected areas. Understanding the effects of human disturbance is essential to this process, but empirical data regarding the effects of human disturbance on Amur tigers is minimal or lacking (Kaplanov 1948; Nikolaev & Yudin 1993; Khramtsov 1995; Matyushkin et al. 1996).

We examined the effect of roads and human disturbance on Amur tigers living on and near Sikhote-Alin State Biosphere Zapovednik (Reserve) in the Russian Far East. Because of its protected status, the Zapovednik provided an opportunity to compare tigers in remote areas with those in areas with human access, including a mostly paved public (primary) road through the Zapovednik and adjacent unprotected areas with secondary road networks. To measure the effect of roads, we compared survivorship and reproductive success of adult female tigers in areas near roads to those in remote areas. To measure one effect of human access, we compared the behavior of tigers of both sexes that were disturbed and undisturbed by people at kill sites. We hypothesized that (1) female tiger survivorship and reproductive success is lower for tigers living in close proximity to roads and (2) tigers forage less efficiently when disturbed by humans at kill sites. Although we recognize that human access may have a variety of negative effects beyond the scope of our research, these two types of disturbances are prevalent in both unprotected and protected areas and have management implications for tiger conservation.

Methods

Study Area

We studied tigers on and near the 390,184-ha Sikhote-Alin State Biosphere Zapovednik (hereafter, Zapovednik), Primorye Krai (province) (Fig. 1). Russian Zapovedniks are highly protected lands with minimal human disturbance; access is restricted to scientists and forest guards (Miquelle et al. 1996; Stepenitski 1996). The land surrounding the Zapovednik is sparsely populated (about 13,000 people live in five villages) and includes a 70,350-ha buffer zone ranging from 1 to 8 km wide. Human activities allowed in the buffer zone include fishing, hunting, tourism, and some agricultural practices such as livestock grazing and hay cutting. The region is primarily forested, the most common forest types being secondary Mongolian oak (*Quercus mongolica*) and birch (*Betula* sp.) upland forests, Korean pine (*Pinus koraensis*) forests, and spruce (*Picea ajanensis*)-fir (*Abies nephrolepis*) and larch (*Larix dahuricus*) forests.

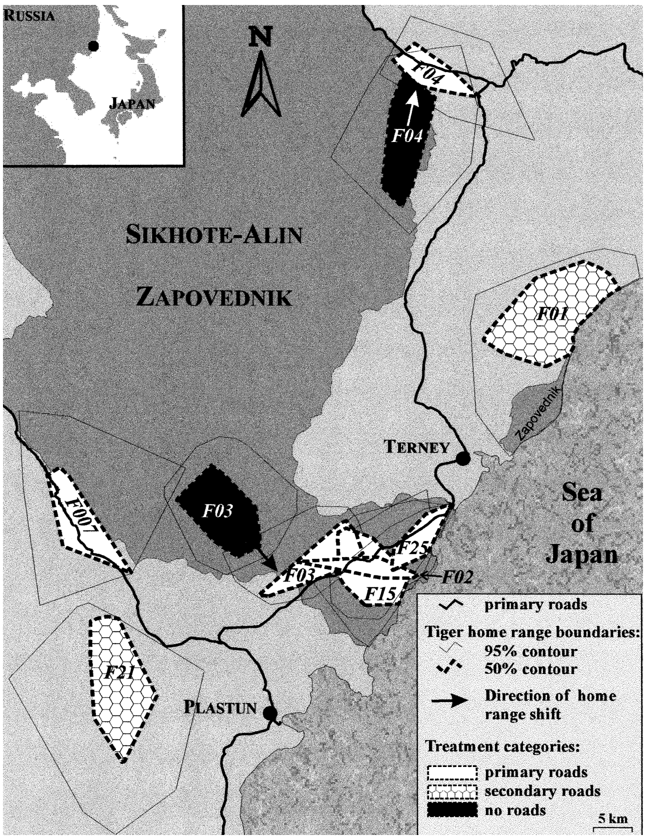

Figure 1. Map of study area showing tiger home ranges (50% and 95% convex polygons) in relation to their overlap with roads in and near the Sikhote-Alin State Biosphere Zapovednik, Primorye Krai, Russia, 1991–2000. Secondary roads were not mapped because they are numerous and their locations and numbers change frequently.

Effects of Roads

We defined a road as "primary" if it was maintained year-round and provided access between towns or villages and "secondary" if it was not regularly maintained but allowed public access into forested lands. Primary roads were paved or hard-packed dirt, allowing traffic to move at high speeds, whereas secondary roads were suitable only for four-wheel-drive vehicles for part or all of the year.

Most of the Zapovednik is roadless, but in 1972 a primary road was constructed through 22 km of the southeast section (Fig. 1). Although it is illegal for the public to leave the road corridor, traffic moves unrestricted through the Zapovednik and poaching of ungulates along this corridor is common (Zapovednik records; A. Astafiev, personal communication). Primary roads also border the northeast and southwest boundaries of the Zapovednik. Secondary roads are common in the buffer zone and on much of the state forestry lands adjacent to the Zapovednik. Traffic on primary roads was light during this study: the mean number of vehicles traveling the primary road through the Zapovednik was 4.2 per hour (SD = 3.3, n = 42 hours) between 1801 and 0600 hours and 16.6 per hour (SD = 8.1, n = 18 hours) between 0601 and 1800 hours. Traffic on secondary roads was lighter than that on primary roads and varied greatly with season.

To examine the effects of roads on tiger survivorship and reproductive success, we used data collected from 15 radiocollared tigers (8 adult females and 7 cubs) in and adjacent to the Zapovednik, from 1992 to 2000. Another adult female (F007) was not radiocollared, but we estimated her home range with location data from her two radiocollared male cubs before family breakup. The movements and reproductive status of some of these female tigers were known from snowtracking before their capture (since 1991), and we include these findings. We monitored and collected locations from radiocollared tigers from the ground on foot and in vehicles and from the air in an AN-2 biplane or a MI-8 helicopter. We obtained ground locations by triangulation, by approaching within 100–400 m and partially circling the tiger, by visual observation, and by subsequently locating tracks in an area where we detected a tiger from its signal. During the first 3 years of work, we flew to locate animals approximately once every 10 days, but later in the study when aircraft availability declined, we flew less frequently (once every 18 days). We collected locations year-round and most often (95%) during the day.

We estimated 50% (activity centers) and 95% convex polygon (Hayne 1949) home ranges (Fig. 1) for nine adult female tigers (eight radiocollared and one from data collected from her radiocollared cubs) (Fig. 2), with program CALHOME (Kie et al. 1994). The F25 individual was young (estimated 19–26 months) during the study period, so she could have been considered a subadult. But she dispersed from her natal home range, settled in an adjacent area, and demonstrated signs of estrus (vocalizations) and reproductive activity (regularly consorting with a male) (Schaller 1967; Sunquist 1981), so we included her as an adult in our analysis.

To avoid serial correlation, we used locations separated by at least 36 hours and 2 nights, which normally includes several shifts in tiger activity (Yudakov & Nikoleav 1987) and should result in independent locations (sensu Lair 1987; Minta 1993) for a given animal. For most tigers, we estimated home ranges based only on aerial locations to avoid bias associated with locating animals from roads. For F02, F25, and F03 (following her home-range shift), however, the number of aerial locations were too few (4–14 locations) for home-range estimation, so we used locations collected from the ground as well. This may have biased our home-range estimates, particularly for 50% contours, and this potential bias is important because these tigers had activity centers bisected by a primary road. That is, an activity center bisected by a road could be an artifact of our sampling scheme rather than a reflection of the time a tiger spent near a road. For F03 and F25, we examined this potential bias by estimating 50% minimum convex polygon home ranges from data collected during intensive monitoring periods when we attempted to locate both tigers every day (F25 was located on 54 of 56 consecutive attempts and F03 on 37 of 41). Both tigers had 50% contours bisected by a primary road, which indicates that the bias was minimal. Similar data were not available for F02, but considering she had a den site 2 km from a primary road where she stayed with her cubs for 1.5 months of the 4.8 months that she was tracked, we assumed this bias was also minimal for her.

We compared survivorship of cubs (χ^2) and adult female tigers (logistic regression) living in three types of areas (treatments): (1) areas with primary roads, (2) areas containing secondary roads, or (3) areas with minimal or no road access. For statistical comparison we combined treatment areas 1 and 2. We "placed" a tiger into one of these three treatments based on which types of roads bisected its 50% minimum convex polygon home range (Fig. 1). We used data collected from F007 to analyze cub survivorship but not adult female survivorship, because we could not monitor her after cub dispersal. Two tigers (F03 and F04) shifted their home ranges into different treatment areas during our study, and we counted those tigers in both treatments for the amount of time they spent in each. Home-range shifts were characterized by permanent abandonment of ≥50% of the former home range and expansion into adjacent areas. Individual F01 also shifted when she abandoned the northern half of her home range in the spring of 1998, but we ignored this shift in our analysis because it did not result in a change in treatment category and

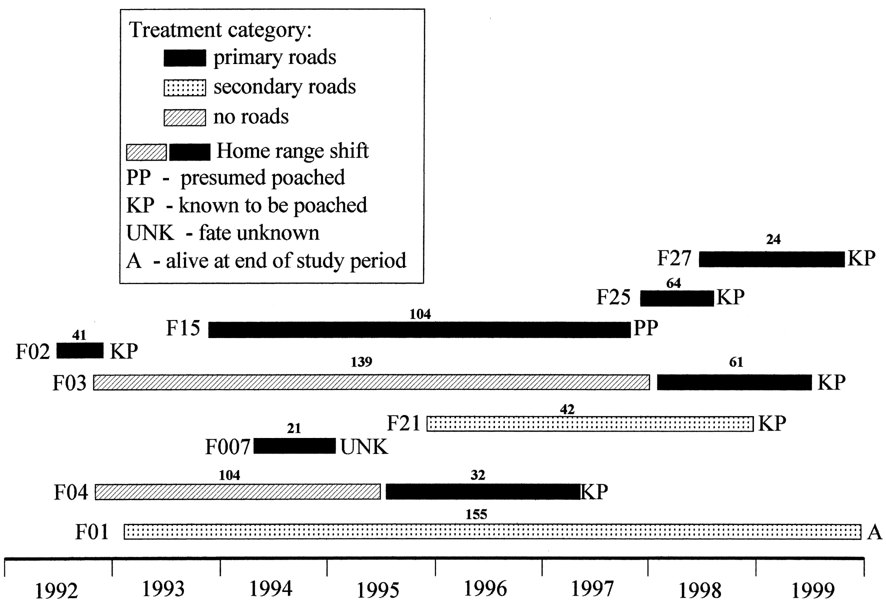

Figure 2. Time span that each of nine adult female tigers was monitored within a home range (Fig. 1) to measure adult survivorship and reproductive success. Monitoring began when a tiger or her cubs (as for F007) were radiocollared and ended with the death or disappearance of that tiger (presumed poached) or the end of the study period. Numbers above bars indicate number of locations used for home-range estimation.

because her second home range was almost completely within the boundaries of her first.

We calculated survival as

$$S = 1 - m\left(\sum_{1}^{i} y_i\right)^{-1}, \quad (1)$$

where y_i is the number of years tiger i was tracked in a given treatment and m is the number of mortalities per treatment at the end of the study period. We constructed this calculation to depict survival as a function of "tiger-years" rather than the annual survival rate used elsewhere (e.g., Heisey & Fuller 1985) because our sample sizes were too small to estimate annual survival. We presumed that F15, who disappeared (Fig. 2), was killed by poachers and her radiocollar destroyed, because we were unable to pick up her signal despite extensive aerial and ground searches and because of tracks in the snow during the first winter following her death. Aerial searches included telemetry flights that covered her entire home range and the home ranges of neighboring tigers (roughly 10,000 km^2 flown every 10 days). Ground searches included daily searches for tracks along a 35-km section of road that bisected the center of her home range and >300 km of foot travel that included at least part of every major drainage in her home range. Intrusions of new tigers (F25 and F03) into her territory provided additional evidence of her death.

Our estimates of adult survivorship within each treatment depended on the time each tiger was monitored, (i.e., probability of a tiger dying increased with time observed). Thus, it was important that the average length of time animals were monitored was similar among treatments or, if not, that they differed in a way that made the test more conservative; in other words, time monitored should be greater in roadless areas. To test this, we compared the mean length of time tigers were monitored in roadless areas to that in areas with roads (primary- and secondary-road treatments combined).

We measured survival rates for cubs from ≥2 months of age, at which time they were able to travel with their mothers and were detectable by tracks, to the age of family breakup (Smith 1984; Smirnov & Miquelle 1999). We considered cubs to have survived if evidence (radio signals or, for uncollared cubs, tracks) indicated they were still in association with their mother at 15 months of age, the minimum age of family break-up (L.L.K. et al., unpublished data). If we knew a female tiger was traveling with at least one cub but we were unable to determine the exact litter size before it perished, we considered it to be a litter of one because of our statistical analysis of cub survival. We defined reproductive success as the number of cubs a female tiger produced that survived to family breakup. We used this definition because most of the cubs were monitored only until family breakup and, in most cases, we did not know if after leaving their mothers they survived to be successfully recruited into the population.

Human Disturbance at Kills

We studied the effects of human disturbance on tiger foraging efficiency and behavior at kill sites from March 1995 to May 1998. We defined foraging efficiency as the amount of meat eaten from each kill made. We considered a tiger disturbed if a person or persons approached the kill close enough to be detected by the tiger (disturbance distance ranged from 5 to 200 m) and a kill abandoned if a tiger left and did not return following disturbance. We monitored kills for at least 2 days to determine whether or not a tiger returned. Radiocollared and unmarked tigers were disturbed by Zapovednik staff, hunters, film crews, capture attempts, and accidental intrusions by our research staff.

We located tiger kills with a variety of methods. Most commonly, we used radiotelemetry (Miquelle et al. 1996) to determine if a tiger had remained in one place for more than 1 day. We investigated the site after the tiger left. We also found kills by following tiger tracks in snow (Yudakov & Nikoleav 1987), by searching areas with congregations of scavengers such as ravens (*Corvus corax*), crows (*C. cornix* and *C. macrorhynchos*), and eagles (*Haliaeetus albicilla* and *H. pelagicus*), through chance encounters, and from reports of forest guards, hunters, or other field workers. At kill sites, we recorded evidence of human disturbance (e.g., footprints), and, because it is not uncommon for people to take meat from tiger kills, we looked for knife or axe marks on kill remains. We determined that a tiger was disturbed while at a kill site by (1) directly observing people and tigers at kills, (2) monitoring radio signals while people approached a kill, and (3) examining a kill site after a person or persons had reported finding a tiger at a kill and determining the timing of abandonment relative to human disturbance from tracks and information provided by the observer. If we were unsure as to whether people approached a kill when the tiger was present or after it had already left the area, we did not use that kill in our analysis.

We visually estimated the percentage of meat eaten by tigers from each carcass by considering that 25% of the meat on a carcass was either (1) a hind leg and half of the body up to but not including the rib cage or (2) a front quarter (a leg, half the neck and head, and half the body including rib cage and internal organs). The percentage of meat not eaten from a carcass was equal to the estimated sum of the meat left on each quarter.

We compared two factors at tiger kill sites disturbed and undisturbed by humans: (1) percentage of meat eaten from each kill and (2) time tigers spent at kills (Wilcoxon matched-pairs test; Ambrose & Ambrose 1981).

To determine whether tigers move less when on kills, we compared average distances between sequential daily locations of four different tigers when they were on kills to those when they were not on kills (Wilcoxon matched-pairs test; Ambrose & Ambrose 1981). Daily locations were those taken approximately 24 hours apart.

Results

Effects of Roads

There was no difference between the mean time tigers were monitored in roadless areas ($\bar{x} \pm$ SD = 4.0 ± 1.8 years, $n = 2$) before they shifted their home ranges and the time tigers were monitored in other treatments ($\bar{x}$ = 2.3 ± 2.1 years, $n = 9$, $t = 2.3$, df = 9, $p = 0.32$) before they died, disappeared, or the study period ended (Fig. 2). Although because of small sample sizes we may have failed to detect a difference, tigers were monitored longer in roadless areas, which should make our test for differences in survivorship more conservative.

Adult female survival per tiger year was greatest (logistical regression, $\chi^2 = 12.2$, df = 2, $p < 0.002$) for radiocollared tigers in roadless areas (Table 1; Fig. 2), but parameter estimates were unstable because our sample size in roadless areas was small. All adult female tigers in roadless areas ($n = 2$) survived their tenure in those locations, whereas all living in an area with primary roads ($n = 6$) were poached (Fig. 2). One tiger (F21) was poached in an area with secondary roads.

The F25 and F27 individuals were not included in the analysis of cub survival because they did not survive long enough in areas with primary roads to reproduce. Cub survival was lower in areas with primary and secondary roads than in roadless areas ($\chi^2 = 10.9$, df = 1, $p = 0.009$; Table 1). Of ≥9 cubs that died in areas with primary roads, 1 was hit by a vehicle, 4 were removed from the wild when their mother (F02) was poached along the road, we presumed ≥1 died of starvation at 3.5 months of age when their mother (F15) was poached, and 3 died of unknown causes (Table 1).

Of the eight cubs that survived to 15 months in areas with primary roads, 1 was killed by a collision with a truck at 20 months; she had not left her natal home range. Another cub (F23), which was captured and radiocollared, survived to adulthood, but her mother (F4) was killed by poachers shortly after family breakup. We also radiocollared three additional survivors from two litters, all of which dispersed from their natal home ranges.

Of 6 cubs that died or were "lost to the population" in areas with secondary roads, 2 died of unknown causes at <1 year, one 6-month-old was shot when it attacked a forest guard, and three 7-month-old cubs were provided with supplemental feeding after their mother was poached. We considered these three cubs lost to the population (mortality) because they would have died without human intervention. Nine of 10 cubs survived to family breakup in roadless areas (Table 1). Only 1 cub died, of unknown causes, at approximately 5 months. Of the 9 survivors, 3 were radiocollared and survived past 20 months, and dispersed from their natal home ranges.

Disturbance at Kills

We monitored 15 tigers (11 with radio collars and 4 without) on 86 kills (Table 2) and examined kill sites after tigers departed. In the absence of human disturbance, tigers consumed more meat from each kill ($\bar{x} \pm$ SD = 97 ± 9% meat eaten, $n = 62$ kills) than tigers disturbed at kills ($\bar{x}$ = 64 ± 32% meat eaten, $n = 24$ kills; $Z = 3.71$, $p = 0.0002$). Undisturbed tigers also spent more time at each kill site ($\bar{x}$ = 3.3 ± 1.5 days; $n = 60$) than disturbed tigers ($\bar{x}$ = 2.4 ± 1.6 days, $n = 25$; $Z = 2.3$, $p = 0.02$). Abandonment of kills occurred in 63% of 24 instances when tigers were disturbed by people. Individual tigers varied in their response to human disturbance, however (Table 2). Eight tigers were more tolerant to human disturbance, returning to 9 kills and eating after people left. Six tigers did not return to 15 kills after being disturbed, even though ≥70% of the meat remained on 11 of the 15 kills. One female (F15) with a 1-year-old cub was disturbed at 8 sequential kills and abandoned all of them. Distance between daily locations was significantly smaller for 4 tigers when they were on a kill than when they were not (Table 3).

Table 1. Survival of cubs and radiocollared female tigers in areas with and without roads on and near the Sikhote-Alin State Biosphere Zapovednik, Primorye Krai, Russia, 1991–1998.

Treatment	*Females* n	*Tiger-years*[a]	*Female survivorship per tiger-year*	*Litters* n	*Cubs produced*	*Cubs surviving to age of family breakup*
Primary roads	6/5[b]	10.6	0.33	7	17[c]	8[d]
Secondary roads	2	9.9	0.90	4	10	4
Roadless	2	8.0	1.00	4	10	9

[a] *Tiger-years represent the sum of the number of years that each tiger was tracked in each different area.*
[b] *Six females were used to determine adult mortality rates, and litters from five females were used to determine cub survivorship.*
[c] *There were 17 or more cubs because one litter had an unknown number of cubs (≥1). However, we used* n = 17 *for statistical analysis of cub survival.*
[d] *One of these eight was killed by a truck when she was 20 months old and before she dispersed from her natal home range.*

Table 2. Disturbance level and response by 15 individual tigers at 86 kill sites on and near the Sikhote-Alin State Biosphere Zapovednik, Primorye Krai, Russia, 1995–1998.

			Break down of total kills		
Tiger	*Sex*	*Number of kills*	*undisturbed*	*disturbed*	*abandoned after disturbance (%)*
01	F	16	16	0	
03	F	10	9	1	0
04	F	2	1	1	0
15	F	22	14	8	100
16	M	13	10	3	66
18	M	1	0	1	100
20	M	5	2	3	33
21	F	2	1	1	0
22	M	3	3	0	
23	F	1	0	1	100
25	F	6	5	1	0
unmarked	F	1	1	0	
unmarked	F	2	0	2	100
unmarked	M	1	0	1	0
unmarked	F	1	0	1	0
Totals		86	62	24	

Discussion

Although our sample size was small for adult female tigers in roadless areas ($n = 2$) and both tigers left these areas during the study, we consider this a valid "control" group to compare with "treatment" tigers in areas that contain roads because (1) both tigers lived in both treatment types (Fig. 2) long enough to have reproduced (both produced two litters in roadless areas and one litter in areas with primary roads) and (2) there was no difference between the time tigers were monitored in roadless areas before they shifted and the time tigers were monitored in other treatments before they died or the study ended.

Our data support the hypothesis that the risk of adult female mortality increases and reproductive success decreases for tigers whose territories include primary roads. An area of particular concern was that portion of the Zapovednik bisected by a primary road. Over an 8-year period, all four adult female tigers holding territories in that area were poached or presumed poached, and no cubs born in that area survived to dispersal age, except one radiocollared male cub (15 months old and alive at the time of manuscript preparation) and his sister, whose present status is unknown. Although our sample sizes were small and our study represents only one region within Amur tiger range, the data indicate that tigers living in the vicinity of lightly traveled primary and secondary roads incurred greater mortality and lower reproductive success than those with territories away from roads. Because it is protected, the Zapovednik supports a greater abundance of prey and higher tiger densities than surrounding unprotected areas and acts as a source population for tigers (Smirnov & Miquelle 1999; Miquelle et al. 1999). Our data suggest, however, that construction of the road through the southeast section of the Zapovednik resulted in an otherwise high-quality habitat becoming a population sink for tigers and providing no recruitment of young animals into adjacent areas. It is almost certain that these effects would be greater in areas where road traffic is heavier.

Amur tigers are territorial (Matyushkin et al. 1980; Yudakov & Nikoleav 1987; Salkina 1993; Goodrich et al. 1999; Miquelle et al. 1999), and home-range shifts made by tigers F03 and F04 during our study were likely a result of (1) daughters inheriting their natal home ranges as mothers shifted to other areas, as described by Smith et al. (1987), and (2) territories concurrently becoming vacant in adjacent areas with primary roads. For example, tiger F15 took up residency in an area with a primary road (Fig. 1) after the former resident, F02, was poached and that territory became vacant. Likewise, tigers F25 and F03 took up residency in portions of that area after tiger F15 disappeared and was presumed poached, F03 residing in a territory in the southern half of the area and F25 in the northern half.

Tigers may also be attracted to roads, as evidenced by individuals in our study whose activity centers included

Table 3. Comparison of mean distance between daily locations of radiocollared tigers on kills and those not on kills in and near the Sikhote-Alin State Biosphere Zapovednik, Primorye Krai, Russia, 1995–1998.

	Mean distance moved (km)			
Tiger	*on kill* (n)	*not on kill* (n)	Z	p
F01	0.1 ± 0.2 (8)	3.6 ± 2.4 (8)	2.5	<0.05
F03	0.07 ± 0.2 (22)	4.3 ± 2.1 (19)	3.8	<0.001
F15	0.2 ± 0.2 (25)	5.7 ± 3.4 (25)	4.4	<0.0001
M16	0.7 ± 1.1 (17)	7.9 ± 4.8 (20)	3.6	<0.001

roads (Fig. 1). Amur tigers and other large carnivores use roads as travel corridors (Matyushkin 1977; Bragin 1986; LeFranc et al. 1987; Bailey 1993; L.L.K. et al., unpublished data), exposing themselves to poachers and fast-traveling vehicles. After tiger F03 shifted from a roadless area to an area with a primary road, she was observed several times walking on the road during daylight hours, showing no apparent fear of traffic. Khramtsov (1995) reported that over a 10-year period, six Amur tigers were shot and killed by poachers along a road near Lazovsky Zapovednik.

The detrimental effects of roads have been reported for a wide variety of large carnivores (Noss et al. 1996; Table 4). Because large carnivores occur at low densities and have low reproductive rates, the effects of human disturbance are often magnified. Small changes in reproductive success and survivorship can have serious implications for isolated carnivore populations (Knight & Eberhardt 1985). Roads are a serious threat to many large-carnivore populations because they facilitate human access, thereby increasing disturbance, decreasing available habitat, decreasing reproductive success, and increasing mortality rates. Increased human-related mortality (Murphy 1983; Maehr et al. 1991), decreased prey abundance (Caro 1994), habitat degradation (Smith et al. 1998), and avoidance of otherwise suitable habitat (review by Weaver et al. 1996) have all been attributed to road access or high road densities.

The effect of roads can vary among large-carnivore species and among sex and age classes within species (Table 4). For example, female Florida panthers (*Puma concolor coryi*) avoid crossing roads, which thereby become barriers that delineate territorial boundaries and affect spacing patterns. Male panthers readily cross roads, however, resulting in relatively high mortality rates from vehicle collisions (Maehr 1997). Gray wolves (*Canis lupus*) shift territorial boundaries to avoid heavily traveled roads (Thurber et al. 1994), whereas female grizzly bears (*Ursus arctos*) with cubs may be attracted to habitats adjacent to roads because males avoid those areas (Mattson et al. 1987).

Human-induced mortality can have deleterious effects on a population beyond the loss of a breeding individual

Table 4. Documented deleterious effects of roads on large carnivores.[a]

		Increased human access resulting in				*Habitat alterations*	
Species	*Behavioral response*	*aggressive encounters with humans*	*overharvest*	*displacement*	*vehicle collisions*	*habitat loss*	*habitat fragmentation*
Canidae							
Gray wolf (*Canis lupus*)[b]	+/− +/−		+	+	+	+	+
Ursidae							
Grizzly bear (*Ursus arctos*)[c]	+/+ +/−− −/− /+	+	+	+	+	+	+
American black bear (*U. americanus*)[d]	0/− −	+	+	+	+	+	+
Spectacled bear (*Tremarctos ornatus*)[e]			+			+	+
Asian black bear (*U. thibetanus*)[f]		+	+			+	
Felidae							
Tiger (*Panthera tigris*)[g]	+ +					+	
Lion (*P. leo*)[h]			+				
Cheetah (*Acinonyx jubatus*)[i]			+[j]	+			
Cougar (*Puma concolor*)[k]	+		+		+		
Florida panther (*P. c. coryi*)[l]	0 −		+		+		+
Iberian lynx (*Lynx pardina*)[m]	+ +				+		+

[a]*Where behavioral responses were reported in the literature we scored them as follows: −, avoidance of roads; +, attraction to roads; or 0, no response.*
[b]*Mladenoff et al. (1995); Thiel (1985), Wisconsin; Fuller et al. (1992), Minnesota; Thurber et al. (1994), Alaska.*
[c]*Review by Servheen (1987), widespread; Mattson et al. (1987), Wyoming; McLellan & Shackleton (1988), Rocky Mountains; Mace et al. (1996) and Kasworm & Manley (1990), Montana.*
[d]*Singer & Bratton (1980), Tennessee; Manville (1983), Michigan; Brody (1984), North Carolina; Young & Beecham (1986), Idaho.*
[e]*Peyton (1994), Peru.*
[f]*Hazumi (1994), Japan.*
[g]*Smith et al. (1998), Nepal; Matyushkin (1977), Russia.*
[h]*Schaller (1972), Serengeti, Africa.*
[i]*Caro (1994), Serengeti, Africa.*
[j]*Overharvest of game species.*
[k]*Murphy (1983), Montana; Beier (1995), Southern California.*
[l]*Maehr (1997); Maehr et al. (1991), Florida.*
[m]*Ferreras et al. (1992); Rodriguez & Delibes (1992), Spain.*

and its progeny. The loss of tenured individuals from populations of solitary carnivores, especially in those with territorial systems, may result in social instability, increased aggressive interactions and associated mortality, increased infanticide, decreased reproduction, and increased disease (Smith 1984; Hornocker & Bailey 1986; Smith & McDougal 1991; Goodrich & Buskirk 1995). Also, high survival and longevity of adult females is critical to the continued well-being of most carnivore populations (Smith & McDougal 1991; Weaver et al. 1996).

Using a tiger population simulation model, Kenney et al. (1995) found that when poaching continued over time, the probability of population extinction increased sigmoidally. Other forms of persistent human-induced mortality would presumably have similar effects. Although evidence is biased toward greater detectability of human-related mortality, Matyushkin et al. (1996) reported that most tiger mortality in the Russian Far East is human-related. Our data support these findings and demonstrate that roads increase tiger mortality due to poaching and traffic accidents.

Tiger conservation in Russia must include prevention of road construction wherever possible, closing unnecessary roads, and regulating access to roads through sensitive areas, particularly in areas supporting source populations (Smirnov & Miquelle 1999). Examples of how road closures have protected wildlife habitat and increased wildlife populations could act as models for the Russian Far East (Mattson 1993; Willcox & Ellenberger 2000). A key to halting further decline in tiger numbers throughout their range would be the establishment of a landscape-scale plan that protects existing tiger habitat and provides for the needs of local people (Smith et al. 1998; Miquelle et al. 1999). Regulating road access through tiger habitat should be an important component of any management regime on tiger-management areas.

Our data support the hypothesis that tigers forage less efficiently when they are disturbed by humans at kill sites. Disturbed tigers ate less from each kill because they often abandoned kills, whereas undisturbed tigers rarely left until all meat was consumed. Tigers at kills moved less and hence probably expended less energy than those not on kills, while realizing an energy gain by remaining longer and consuming all available meat on kills. Frequent disturbance of individual tigers may increase energetic demands because tigers are forced to eat less from each kill and spend more time hunting and less time resting. Although we have no direct evidence, this could result in increased risk of injury and death associated with predation attempts (Rabinowitz 1986; Mech & Nelson 1990), reduced reproductive success, and reduced survival of both adults and cubs whose mothers are disturbed frequently.

Reduced feeding activity and increased energy expenditure in response to human recreational activity have been documented for a variety of species, including Bald Eagles (*Haliaeetus leucocephalus*), bighorn sheep (*Ovis canadensis*), and mule deer (*Odocoileus hemionus*) (MacArthur et al. 1979; Stalmaster & Newman 1978; Freddy et al. 1986; Stalmaster & Kaiser 1998). Black bears (*Ursus americanus*) sometimes abandon their dens in response to human approach (LeCount 1983; Hellgren & Vaughan 1989; Goodrich & Berger 1994), resulting in greater overwinter weight loss (Tietje & Ruff 1980), cub abandonment, and cub mortality (Goodrich & Berger 1994). Amur tigers are frequently disturbed at kills in winter because their tracks are easy to follow and crows and eagles around carcasses make kills conspicuous.

Our data are not suitable for examining the relationship between human disturbance at kills and the vicinity of kills to roads because our ability to detect and monitor disturbance and tiger behavior at kills was closely related to distance to roads. Moreover, our data do not reflect disturbance rates.

Because tigers often use roads as travel corridors, tigers displaced from their kills not only lose a valuable food resource, they are at greater risk of being poached or killed in traffic collisions because they may be on the road more often. In addition, tigers may be more at risk of being displaced or being poached while on their kills in areas with roads because tigers can be more easily tracked to kills, as with F21, who was shot 1 km from a secondary road after a poacher tracked and shot her while she and her three cubs were at a kill site.

Although some tigers may become habituated to human disturbance (McDougal 1977), habituation may lead to increased aggressive encounters with people, as with grizzly bears (Mattson et al. 1996) and Asiatic lions (*Panthera leo persica*) (Saberwal et al. 1994). Bait-site feeding of tigers for public viewing was halted in Chitawan National Park, Nepal, after two tiger attacks on humans (McDougal 1977). Public attitudes toward carnivores affect conservation efforts (Kellert et al. 1996), and increased aggressive encounters may weaken public support for tiger conservation in the Russian Far East. News of tigers in close proximity to villages and encounters between tigers and hunters are nearly always reported in local newspapers and journals (e.g., Smirnov 2000).

Our data suggest that, in the absence of human disturbance, Amur tigers usually consume nearly all available meat at kills. The misconception of frequent surplus killing among tigers in the Russian Far East has probably arisen because tigers often abandon kills when disturbed by people (in such cases the observers of surplus killing) and people often usurp meat from kills, making it necessary even for those tigers that return to kills to hunt again. For example, Pikunov (1983) reported snow-tracking a tiger that killed five ungulates in 15 days and never ate more than 20% of any of them. This is likely an artifact of repeated disturbances of sequential kills by the observer and not typical tiger behavior.

Conclusions

The effects of human disturbance on the survival and foraging of tigers can be mitigated through appropriate management actions. Roadless areas with minimal and regulated human access should be maintained throughout the range of the Amur tiger to avoid mortalities from auto collisions and poaching and to minimize human disturbance to tigers. This is particularly important in areas such as national parks and Zapovedniks that are considered source populations. Human activities should also be restricted in sensitive areas and time periods, such as when resident females are traveling with young cubs. Education programs, particularly those directed at visitors to national parks and Zapovedniks, should stress the importance of avoiding tiger kills. Whenever possible, roads through protected tiger habitat should be closed at night and speed limits should be strictly enforced.

The implications of our results may be most important in unprotected areas where human access to tiger habitat is unrestricted and human behavior more difficult to regulate. We encourage the development of programs for closing secondary roads no longer being used for resource extraction and for restricting the construction of new roads through sensitive tiger habitat as important measures to protect Amur tiger populations.

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