



Comparison of methods for estimating Amur tiger abundance

Authors: Riley, Meghan, Soutyrina, Sveta, Miquelle, Dale, Hayward, Gregory, Goodrich, John, et al.

Source: Wildlife Biology, 2017(1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00253>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Comparison of methods for estimating Amur tiger abundance

Meghan Riley, Sveta Soutyrina, Dale Miquelle, Gregory Hayward, John Goodrich and Steven Buskirk

M. Riley (meghan.d.riley@gmail.com) and S. Buskirk, Univ. of Wyoming, 1000 East University Avenue, Laramie, WY 82071, USA.

– S. Soutyrina, Sikhote-Alin Biosphere Zapovednik, Terney, Primorski Krai, Russia. – D. Miquelle and J. Goodrich, Wildlife Conservation Society, Bronx, NY, USA. DM also at: Far Eastern Federal Univ., Ayaks, Russki Island, Vladivostok Russia. – G. Hayward, Univ. of Wyoming, Laramie, WY, USA

The Amur tiger *Panthera tigris altaica* is endangered throughout its range. Estimating abundance to monitor population trends is needed to judge success of conservation efforts. However, low densities and elusive behavior make precise estimates difficult to achieve. Managers must employ sampling methods that maximize precision while remaining feasible under constraints inherent to areas tigers inhabit. We applied camera trap, hair snare, DNA collection, scent-matching dog, morphometric track identification and track survey methods and developed a rubric to evaluate their efficacy in estimating tiger abundance in Russia. We conducted sampling over the course of one year in Sikhote-Alin Biosphere Zapovednik (SABZ). We ranked candidate methods using logistical, statistical and cost criteria to evaluate their efficacy for monitoring tiger numbers. Due to logistical and technical constraints, we relied on data from a parallel study to derive three statistical criteria for the DNA collection method. Camera traps, DNA collection, and track surveys were the only methods with sufficient sample sizes to estimate abundance for each sampling session during which the method was tested. DNA collection and camera traps were promising statistically, though poor-performing for logistics and cost. Technical improvements in camera trap design since the time of this study may improve the method's statistical and cost performance compared to our evaluation. Conversely, track surveys were most efficient logistically and financially, but poor statistically. Method choice for any given monitoring situation should consider local conditions and the specific objectives of the monitoring program in light of all three criteria – statistical, logistical and cost. Failure in any of these areas can lead to failure of a monitoring program.

Monitoring trends in abundance is fundamentally important for endangered species and is the starting point for practitioners seeking to implement recovery plans. Sparsely distributed, forest-dwelling carnivores such as the Amur tiger *Panthers tigris altaica* are especially difficult to enumerate (MacKenzie et al. 2005). The Amur tiger is endangered throughout its range, due primarily to poaching (Robinson et al. 2015) and prey depletion (Miquelle et al. 1999). Only 3.4% of Amur tiger range occurs in strictly protected areas, leaving most tigers vulnerable (Carroll and Miquelle 2006). Unfortunately, estimating Amur tiger abundance is particularly challenging due to heavily forested habitat, low tiger densities, and the elusive nature of tigers. Low prey biomass in the Russian Far East (RFE) (Stephens et al. 2006) demands that tigers maintain large home ranges to find adequate food (Goodrich et al. 2010, Miquelle et al. 2010). Accordingly, densities (0.1–1 tigers/100 km²) can

be an order of magnitude lower than those of subspecies in more productive forests of southeast Asia and southern Asia (Soutyrina et al. 2013, Miquelle et al. 2015). These biological realities are compounded by logistical issues associated with fieldwork: remote forested habitat, low road densities, severe weather and limited transportation (e.g. poor availability of air service).

Historically, biologists estimated Amur tiger abundance through track surveys conducted as a synchronized effort by hundreds of field technicians across the entire subspecies range. Despite developing an algorithm to standardize interpretation of track counts (Miquelle et al. 2006), with no estimate of detectability and no validation of expert track interpretation methods, accuracy of this approach is unknown. Due to the difficulty of mounting range-wide surveys regularly, biologists conducted a monitoring program over 16 monitoring units from 1997 through 2011 relying on two indicators of abundance that were generally well correlated: 1) an index of abundance derived from track data that included an estimate of error; and, 2) the traditional interpretation of track data based on expert assessment (Hayward et al. 2002). However, due to difficulties in application of even validated indices (Anderson 2001) and the

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <<http://creativecommons.org/licenses/by/4.0/>>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

clear benefits of accurately monitoring population size, finding a method to estimate absolute abundance and associated sampling variance is of paramount importance.

Numerous non-invasive methods are suitable for carnivore monitoring (Wilson and Delahay 2001), but many only estimate relative abundance. Sampling approaches that estimate absolute abundance through capture–recapture analyses (Otis et al. 1978, Efford 2016) include camera trapping (Karanth and Nichols 1998), genetic sampling (Belant et al. 2005), morphometric track identification (Sharma et al. 2005), and scent-matching dogs (Kerley and Salkina 2007). Any one of these methods might be suitable for Amur tiger monitoring. However, method evaluation must consider all aspects of application, from field sampling to quantitative estimation. Often methodological research places high emphasis on statistical performance relative to other considerations (Gompper et al. 2006). However, logistical and cultural constraints can be crucial to successful implementation. Therefore, selection of a survey method must consider criteria beyond the statistical properties of the estimator.

We applied six sampling methods under consideration in the RFE including 1) camera trapping (referred to as camera traps), 2) hair snaring for genetic sampling (hair snares), 3) scat and hair collection for genetic sampling (DNA collection), 4) scat collection for identification by scent-matching dogs (scent dogs), 5) morphometric track identification (track ID), and 6) an algorithm using traditional track survey data (track survey). All methods estimate abundance using capture–recapture analysis with the exception of track surveys, which can be applied to cover much greater geographic areas. Although the algorithm coupled with traditional track survey data only determines a minimum number of tigers, it is included in this study because it represents the current approach and serves as an informative baseline relative to other methods. Our objectives were to implement all six methods concurrently for one year in Sikhote-Alin Biosphere Zapovednik (SABZ) and assess the overall feasibility of each method by comparing logistical, statistical and cost constraints. It was not feasible to estimate abundance for some methods due to small sample size (hair snares, track ID) or the inability to analyze samples (DNA collection). However, we included these methods in our analysis because our intent was not only to assess statistical performance, but also logistical and financial limitations of methods applied in a real-world context with a subspecies of high conservation concern. We crafted our evaluation to identify a pragmatic sampling approach, taking into account circumstances specific to the RFE. Furthermore, the approach we used to assess feasibility of a method is applicable for managers seeking to identify appropriate survey methods for other species under other conditions.

Material and methods

Study area

We conducted the study in SABZ, an IUCN category Ia scientific reserve in the RFE (44°46'N, 135°48'E). The reserve is in the central portion of Amur tiger distribution

and serves as a source population for the subspecies (Carroll and Miquelle 2006). The reserve covers approximately 4000 km², dominated by the Sikhote-Alin Mountains. SABZ contains three major river basins: Djigitovka (876 km²), Serebryanka (1337 km²), and Kolumbe (1727 km²) (Fig. 1). Along the Sea of Japan coast (Djigitovka), Mongolian oak *Quercus mongolica* woodlands predominate. Further inland on the seaward side of the Sikhote-Alin Mountains (Serebryanka) is a mixed-forest type including deciduous and coniferous species characterized by the presence of Korean pine *Pinus koraiensis*. On the west side of the Sikhote-Alin Divide (Kolumbe), a boreal forest of spruce *Picea ajanensis*, fir *Abies nephrolepis* and larch *Larix daburica* predominates (Stephens et al. 2006). Summer is mild with low precipitation from May to early July, followed by a monsoonal stage from late July through September. Winter exhibits a more uniform climate dominated by cold, dry air from Siberia, resulting in frequent winds. Temperatures range from 15°C in summer to –14°C in winter. Snow was present from November through April, at depths ranging from near 0 m along the coast to over 1 m at higher elevations.

Candidate methods

We applied six methods from June 2007 through July 2008. Ten technicians assisted in sampling, except for the track survey, which was carried out exclusively by reserve staff. We examined the logistical feasibility, quality of data collected, and cost for each method. We used these data to develop a rubric to compare efficacy of the methods to estimate tiger abundance relative to each other.

Sampling sessions

We sampled SABZ between June 2007 – July 2008. We sampled Serebryanka in summer 2007, Djigitovka in fall 2007 and winter 2008, and Kolumbe in spring 2008. We implemented camera trap, hair snare, DNA collection, and scent dog methods concurrently in all four sampling sessions. We applied track ID and track survey methods only during the winter sampling session. We divided each basin into 49-km² grid units to guide placement of sampling stations (camera traps, hair snares) and survey routes (DNA collection, scent dogs, track ID). The track survey followed traditional survey routes without consideration of grids, but covered the reserve's three major drainages. We checked sampling stations and routes every two weeks with the exception of the traditional track survey.

Camera traps

We deployed camera traps at 68 sites (Serebryanka: n = 24, Djigitovka: n = 22, Kolumbe: n = 22). We spaced camera trap stations, comprised of paired cameras positioned to photograph both sides of passing tigers, at one station per grid cell. We oriented cameras at slightly different angles or offset them a short distance from each other to minimize backlighting from flashes. We chose sites based on factors likely to increase probability of tiger detection. These included presence of tiger sign such as scent-marked trees (Protas et al. 2010) and placement along travel paths such as riverbanks, hill bases, ridgelines, trails and roads (Matyushkin 1977). We affixed cameras to tree trunks approximately 4



Figure 1. Map of Sikhote-Alin Zapovednik with Djigitovka, Serebryanka, and Kolumbe river basins delineated.

m perpendicular to the tiger's assumed pathway at a height of 0.5 m (Karanth et al. 2002). We deployed CamTrakker (CamTrak South Inc.) and Deercam (Non Typical Inc.) passive infrared cameras and replaced film and batteries regularly. We programmed camera traps to operate 24 h a day. We identified individuals from stripe patterns on their flanks, including adult and subadult tigers. We included all tigers identified in abundance estimates with the exception of cubs.

Hair snares

We deployed hair snares at 151 sites (Serebryanka: $n = 47$, Djigitovka: $n = 54$, Kolumbe: $n = 50$) at a frequency of 1–6 per grid cell, depending on frequency of suitable locations. We chose hair snare locations based on the same factors used for camera traps, in some cases setting hair snares in the same location as camera traps. We affixed snares 0.5 m above the ground on tree trunks adjacent to the tiger's assumed pathway. We constructed hair snares from 10×10 cm sections of short-napped carpet with 3-cm nails protruding from them in summer, fall and winter (Weaver et al. 2005). We used wire cat brushes with protruding metal bristles in spring as materials became available. We baited snares with 5 ml of scent lure (Calvin Klein Obsession for Men perfume), which elicits a cheek-rubbing response in

captive Amur tigers (Riley unpubl.), coating the scent with petroleum jelly to increase longevity. We collected tiger hair using latex gloves and stored samples in envelopes with silica desiccant (McDaniel et al. 2000), replacing used snares to avoid sample contamination.

DNA collection

We established 29 survey routes (Serebryanka: $n = 8$, Djigitovka: $n = 12$, Kolumbe: $n = 9$) through grid cells, traversing them every two weeks in search of hair and scat. In winter, we backtracked tiger tracks for up to 1 km in search of DNA samples. We collected a 2-mm-diameter sample of each scat encountered using latex gloves, placing it in a vial with silica desiccant (McKelvey et al. 2006). We wrapped all remaining scat in aluminum foil, placed in a plastic bag, and froze it to preserve odor for analysis by scent-matching dogs. We collected and preserved all tiger hairs encountered as described above for hair snares.

We were unable to obtain export permits for DNA samples, precluding analyses outside of Russia, and, at the time of this study, lacked access to a laboratory to conduct genotyping in-country, making it impossible to ID individual tigers from samples. We used our own data to assess logistical and cost constraints (consulting with the US Forest Service's Wildlife Genetics Laboratory in Missoula, Montana

to estimate cost), but relied on data obtained by Sugimoto et al. (2012) in the winter of 2002–20003 to provide proxy numeric values for three statistical criteria. Sugimoto et al. (2012) conducted their work in Land of the Leopard National Park, a reserve south of SABZ, using a nearly identical methodology, and collecting a comparable number of samples to those we collected in winter ($n \approx 47$ and $n = 32$, respectively).

Scent dogs

Survey routes, sample area, backtracking protocols, and DNA scat sample collection were the same as described above for the DNA collection method. Dogs trained by Linda Kerley and Victoria Krutova matched scat samples into groups by individual tiger using unique odor signatures of the samples. Four dogs analyzed each sample and an ID was recorded if three of the four dogs made the same ID (Kerley and Salkina 2007).

Track ID

We sampled the same area, using the same routes ($n = 12$) and backtracking protocol followed for DNA collection and scent dogs in search of tiger tracks during the winter sampling session. We photographed suitable tracks encountered along these routes. Following recommendations of Sharma et al. (2005) we measured tracks when all four toes and the notch in the pad were discernible in snow less than a centimeter deep. We placed a ruler beside each track, photographing 10 hind tracks from each track set for future analysis in program PUGMARK 1.0 (Sharma et al. 2005). We measured stride, straddle, snow depth, snow texture and snow moisture when photographing tracks as inputs for discriminant function analysis (Sharma et al. 2005).

Track survey

Reserve staff followed 39 traditional survey routes in search of tiger tracks on two occasions spaced at least a month apart in winter (Miquelle et al. 2015). Because traditional survey routes occurred in fewer minor drainages than the other five methods, a smaller portion of the study area was covered by the track survey. Track surveys commenced ≥ 24 h after snowfall. Observers completed surveys in < 2 weeks, a brief enough period to assume population closure. Survey routes were ≥ 5 km long following trails, frozen rivers and roads within the reserve. Observers recorded date, route length, time since last snow, snow depth, primary forest type and the number and location of tiger tracks that crossed each route. Observers measured front pad width, estimated time elapsed since the track was created in 24-h intervals, and the aspect of the track where it crossed the survey route (Hayward et al. 2002). An algorithm using 1) average daily travel distances for Amur tigers, 2) maximum likely movement distances given known home range sizes, 3) pad width, 4) distance between tracks, and 5) track age input into ArcMap and Microsoft Access (Miquelle et al. 2006) estimates a minimum number of Amur tigers for the survey area.

Method comparison

Comparison rubric

We compared methods using a rubric exploring 3 broad criteria: 1) logistical constraints encompassing physical, cultural, and political barriers to implementation; 2) statistical precision, bias, and complexity; and 3) cost in money, time, and personnel of establishing and implementing the method. Under each of these criteria, we examined sub-criteria that would influence performance of a given sampling method (Table 1). We ranked methods from best to worst for each

Table 1. Comparison rubric for tiger abundance estimation methods using scores and calculated numeric values for each of 22 sub-criteria grouped into three criteria of interest: logistics, statistics, and cost. Scores from 1 to 4 represent a scale of difficulty, variability, bias, or complexity (1 = none, 2 = slight, 3 = moderate, 4 = extreme).

Criterion	Sub-criterion	Score/value	Notes	
Logistics	difficulty covering sampling sites	1 – 4	distance to sites, frequency of checks, no. of seasons sampling possible	
	geographic coverage	0 – 100%	area sampled (sampled area \div by reserve area)	
	difficulty of gear transport	1 – 4	gear mass, no. items necessary per sampling site	
	difficulty of site setup	1 – 4	set-up time, potential for malfunction due to poor setup	
	performance variability	1 – 4	degree sampling apparatus/observer variability leads to missed/mistaken IDs	
	difficulty of protocol	1 – 4	no. of steps, technical knowledge needed to implement, cultural resistance to collection of field data	
	difficulty of bureaucratic process	1 – 4	effort to procure local permissions	
	difficulty of permitting process	1 – 4	effort to procure national and international permits	
	Statistics	precision (CI)	tigers	tigers between upper and lower bounds of 95% CI
		precision (net capture probability)	0 – 100%	probability tiger i will be captured at time j
bias (population closure)		–5 – 5	z-statistic from closure procedure in secr	
bias (failure of field/lab techniques)		1 – 4	probability of apparatus malfunction, theft, misidentification of tigers	
complexity of sampling design		1 – 4	identification of population of interest, defining sampling frame, conceiving means of sampling	
Cost	complexity of analysis	1 – 4	intuitiveness, replicability, user-friendliness, no. assumptions	
	personnel	technicians	no. technicians recommended for sampling effort	
	stages of analysis	stages	no. steps between data collection and abundance estimate	
	start-up	USD (\$)	one-time equipment purchases in US dollars	
	annual budget	USD (\$)	salaries, purchased services, equipment repairs, supplies in US dollars	
	data collection	days	no. days from start to finish of sampling session	
	time for analysis	days	no. days to generate abundance estimate after sampling	
	time for permits, sample transport	days	no. days to procure permits and transport samples	

sub-criterion by comparing calculated numeric values (e.g. annual budget) and scores assigned to each method using a four-part scoring system (e.g. difficulty of protocol). For statistical criteria (e.g. 95% confidence interval), we calculated values for each sampling session abundance estimates were possible, then averaged these values for input into the rubric. For logistical and cost criteria (e.g. annual budget), we calculated numeric values for full coverage of the three major drainages in SABZ. When a method did not produce sufficient data to calculate one of the required numeric values, we ranked it below methods with sufficient data for calculation of that sub-criterion. In cases where a numeric value was impossible to calculate for a method, regardless of data, we gave it the worst ranking for that sub-criterion. In cases of ties between methods, we assigned ranks based on a consideration of relative merit for that sub-criterion. For example, the DNA collection, scent dog, track ID, and track survey methods tied for difficulty of gear transport under logistics because no sampling stations were required (in contrast with camera traps and hair snares). Of these, the track ID method received the best rank (1.1) because a GPS unit, data sheets, pencil and ruler were the only gear required for sampling. The DNA collection method received the worst rank (1.4) because collection materials for both scats and hairs were required in addition to a GPS, data sheets and pencil. Furthermore, the DNA method required that scat and hair samples be carried out of the field whereas the track ID method had no physical samples associated with it.

To allow for meaningful comparisons between methods, we calculated three summary metrics. The first metric averaged sub-criteria ranks for each of the three broad criteria, giving each method a mean rank for logistics, statistics and cost. We used this metric to compare method performance for each of the three broad criteria. The second metric averaged all sub-criteria ranks producing 1 mean rank for each method. The third summary metric averaged each of the six method's mean ranks (as calculated for the second metric), producing a single, cumulative mean rank common to all six methods. We subtracted each method's mean rank from the cumulative mean rank to determine which methods performed above average (positive value) and below average (negative value). For criteria deemed critical to a method's success (difficulty of protocol, difficulty of permitting process, precision-CI, precision-net capture probability, annual budget), we weighted these criteria to be twice as powerful in the calculation of mean ranks. In addition, whereas the three summary metrics helped to quantify each method's relative utility, we also based our evaluation on a qualitative assessment of the higher-ranking methods.

Precision and bias

For methods that produced abundance estimates (camera traps, scent dogs), we used 95% confidence interval width and capture probability to evaluate the relative precision of each method. We calculated statistical values using spatially explicit capture–recapture (SCR) models in the R package, secr (Efford 2016). SCR models (Efford 2004, Royle et al. 2009) are less demanding than traditional capture–recapture models in terms of area coverage requirements, making them suitable for species occurring at low densities. We used proximity detectors for methods where detections occurred at discrete locations (camera traps) and polygon detectors for methods where detections occurred over a search area (scent dogs). We used the 'suggest.buffer' function to determine buffer widths to create habitat masks using the trapbuffer method. We defined a sampling occasion as 24-h, modeling the effect of h2 on g0 using starting parameter values provided by autoini to estimate abundance using the 'region.N' function following a halfnormal detection function (Supplementary material Appendix 1 Table A1). As individual heterogeneity models are generally recognized as the most appropriate for analysis of camera trapping and genetic sampling of tigers (Karanth et al. 2011a), we used a two-part finite mixture model in our analysis (Pledger 2000). We tested population closure using the z-statistic (Otis et al. 1978) to measure bias, also assessing how well other assumptions were met using the four-part scoring system described above (Table 1). For the track survey, we had no means to calculate confidence interval, capture probability or z-statistic.

Results

Sampling sessions

Of the six candidate methods, we were able to estimate abundance for camera traps, scent dogs and the track survey. The track survey amassed the largest sample sizes over a sampling period for which population closure could be assumed (Table 2). Camera traps, DNA collection, and scent dogs had the next largest sample sizes respectively, although lacking the means to analyze DNA samples, we were unable to estimate abundance for the DNA collection method using our data. Hair snares only produced samples during one session (n = 5). Given such a small sample size, it is unlikely we could have estimated abundance for the hair snare method had these samples been analyzed. The track ID method failed; only one track set occurred in snow shallow

Table 2. Total samples (n) and tigers identified to individual (tigers) in each sampling session. A sample refers to tracks crossing a survey route (track survey), an individual tiger being photographed at a camera trap site on a given day (camera traps), a scat or hair sample (DNA collection, scent dogs, hair snares), or a track set (track ID). We counted an individual tiger photographed multiple times at a camera trap site on a given day as one sample (n = 1). Dashes (-) denote cases where values could not be calculated.

	Track survey n (tigers)	Camera traps n (tigers)	DNA collection n (tigers)	Scent dogs n (tigers)	Hair snares n (tigers)	Track ID n (tigers)
Summer	– (-)	49 (7)	18 (-)	18 (3)	0 (0)	– (-)
Fall	– (-)	37 (9)	9 (-)	7 (-)	5 (-)	– (-)
Winter	54 (-)	24 (6)	32 (-)	30 (6)	0 (0)	1 (-)
Spring	– (-)	41 (4)	34 (-)	14 (1)	0 (0)	– (-)
Mean	54 (-)	38 (7)	23 (-)	17 (3)	5 (-)	1 (-)

enough to ensure accurate identification using measurements derived from PUGMARK.

Method comparison

Scores and values for each method are reported in Table 3. We generated ranks indicating relative performance from these data, also considering relative merit in the case of ties (Table 4). On average, scent dogs ranked first followed by track surveys and camera traps. These methods had mean ranks better than the cumulative mean rank of all six methods. In contrast, DNA collection, hair snare and track ID methods all had mean ranks worse than the cumulative mean rank for all methods (Fig. 2). Despite these results, high-ranking methods overall may be critically deficient in one or more criteria. No method ranked first for all 3 criteria in our analysis (Fig. 3). The track survey method ranked first logistically and in terms of cost, but ranked low statistically. Similarly, camera traps ranked first statistically, but low in terms of logistics and cost. The remaining methods received more middling ranks across criteria.

Discussion

Wildlife managers have many methods from which to choose to monitor population trends. Decisions regarding which method to use are often dominated by discussions of statistical rigor and likely precision of resulting estimates. Although important, statistical rigor alone is inadequate for method comparison. Many elements influence monitoring success, particularly the ability to collect necessary samples long term. The optimal approach for a monitoring program must consider ecological, cultural and geographic context (Groves

et al. 2002). For instance, a naïve assessment of Amur tiger biology and winter conditions in its range, might identify aerial surveys to locate tiger tracks in snow for backtracking in a probability sampling scheme (Becker 1991) as the most statistically rigorous approach for estimating abundance. However, implementation would likely fail due to visibility issues over a dense canopy and logistical constraints that frequently ground aircraft. Success of methods could vary by season as well, although we lacked sufficient replications of methods in various seasons to systematically address the issue. Therefore managers must consider not just statistical precision, but how the political environment, bureaucratic structure, regionally obtainable tools and biology of the study animal will influence performance. Our comparison rubric can help managers evaluate sampling methods given the realities of local monitoring situations.

Currently, the track survey method has widespread acceptance in Russia, being simple, inexpensive and quick in terms of sampling and analysis. Rapidity of analysis is possible because it is done locally and does not rely on assistance from outside professionals. However, the track survey and minimum tiger algorithm offer no estimates of error or capture probability. These deficiencies are highlighted by the method's poor rubric ranking under statistics. Track survey results rely on expert assessment in addition to the standardized algorithm, and continued debate among Russian biologists in interpreting results of track surveys (Kucherenko 2001), even with the most recent surveys, are a strong indication of the challenges facing this method.

Of the untested methods compared, the scent dog method appeared superior based on its mean rank. Its performance was more consistent under logistical, statistical and cost constraints than other methods. However, there was high variability among observers collecting fecal samples

Table 3. Scores and values assigned to sampling methods (CT: camera traps, HS: hair snares, DNA: DNA collection, SD: scent dogs, TID: track ID, TS: track survey) across logistical, statistical, and cost sub-criteria of the comparison rubric presented in Table 1. Dashes (–) denote cases where values could not be calculated due to insufficient data and “NA” denotes cases where values could not be calculated regardless of sample size.

	Sub-criterion	CT	HS	DNA	SD	TID	TS
Logistics	difficulty covering sampling sites	2	2	3	3	2	2
	geographic coverage	66.3%	66.3%	72.4%	72.4%	72.4%	42.8%
	difficulty of gear transport	4	3	2	2	2	2
	difficulty of site setup	3	2	1	1	1	1
	performance variability	3	2	3	3	4	3
	difficulty of protocol	2	2	4	4	2	2
	difficulty of bureaucratic process	1	1	1	1	1	1
Statistics	difficulty of permitting process	1	4	4	1	1	1
	precision (95% CI width)	12	–	14 ¹	14	–	NA
	precision (capture probability)	37%	–	33% ¹	29%	–	NA
	bias (population closure)	–1.63	–	–0.71 ¹	1.22	–	NA
	bias (field or lab technique failure)	2	3	2	1	2	1
	complexity of sampling design	2	2	2	2	2	2
	complexity of analysis	2	2	2	2	4	4
Cost	personnel	10	10	10	10	10	20
	stages of analysis	3	3	3	3	4	2
	start-up (US\$)	55 420	5990	1965	1960	2265	0
	annual budget (US\$)	19 570	16 475	29 790	15 700	12 515	6610
	data collection (days)	90	90	90	90	90	18
	time for analysis (days)	7	10	93	185	11	2
	time for permits, sample transport	0 days	> 1,000 days	> 1,000 days	0 days	0 days	0 days

1) values from analyses by Sugimoto et al. 2012.

Table 4. Ranks of methods (CT: camera traps, HS: hair snares, DNA: DNA collection, SD: scent dogs, TID: track ID, TS: track survey) for estimating tiger abundance based on scores and values reported in Table 3. Ranks range from 1 (best) to 6 (worst). Where tied ranks necessitated sub-ranking (tens place), sub-ranking was based on qualitative assessment of tied methods' performance. Asterisks (*) denote sub-criteria that were weighted double in calculation of mean ranks.

Criterion	Sub-criterion	CT	HS	DNA	SD	TID	TS
Logistics	difficulty covering sampling sites	1.1	1.1	5	5	1.3	1.2
	geographic coverage	4	4	1	1	1	6
	difficulty of gear transport	6	5	1.4	1.3	1.2	1.1
	difficulty of site setup	6	5	1.2	1.2	1.2	1.1
	performance variability	2.4	1	2.3	2.2	6	2.1
	difficulty of protocol*	1.4	1.1	6	5	1.3	1.2
	difficulty of bureaucratic process	1	1	1	1	1	1
	difficulty of permitting process*	1	5	6	1	1	1
Statistics	precision (CI)*	1	4	2	2	5	6
	precision (capture probability)*	1	4	2	3	4	6
	bias (population closure)	3	4	2	1	4	6
	bias (failure of techniques)	3.1	6	3.2	1.2	3.3	1.1
	complexity of sampling design	1.2	1.3	1.2	1.2	1.2	1.1
	complexity of analysis	1.2	1.2	1.2	1.2	6	1.1
Cost	personnel	1	1	1	1	1	6
	stages of analysis	2	2	2	2	6	1
	start-up	6	5	3	2	4	1
	annual budget*	5	4	6	3	2	1
	data collection	2	2	2	2	2	1
	time for analysis	2	3	5	6	4	1
	time to get permits, transport samples	1	5	5	1	1	1

and marginally adequate sample sizes to conduct analyses. Other studies have had success collecting sufficient scat samples (Mondol et al. 2009) and use of dogs to find scat could increase sample size. However, experienced trainers and dogs providing tiger ID services are scarce, even in Russia where the technique originated, limiting effectiveness of this method.

In our study, camera traps performed poorly in terms of logistics and cost. Cameras can be bulky to transport and vulnerable to malfunction, damage, and theft. These handicaps were not overwhelming, but annual budget was high for camera traps. However, the method ranked first for statistical criteria, and garnered more samples on aver-

age than other capture–recapture methods. Camera traps were further advantageous because analysis could be completed onsite and tiger photographs serve as a powerful tool to connect with and influence politicians and the public. Technical improvements in camera trap design (digital versus film) since the time of this study could improve the method's logistical and cost performance in addition to improving statistical performance by decreasing the likelihood of lost trap nights due to malfunctioning equipment. This, along with longer battery life and a greater storage capacity on memory cards as compared to rolls of film, would likely increase detection rates. Furthermore, high start-up costs associated with this method do not take into account

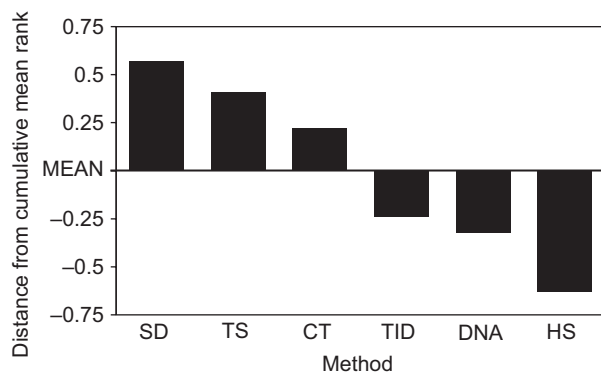


Figure 2. Distances of candidate method mean ranks from cumulative mean rank for all methods (TS: track survey, SD: scent dogs, CT: camera traps, DNA: DNA collection, TID: track ID, HS: hair snares) for estimating Amur tiger abundance (distance = overall mean rank – candidate method mean rank). Ranks range from 1 (best) to 6 (worst). Positive values denote candidate methods with mean ranks superior to the cumulative mean; negative values are inferior.

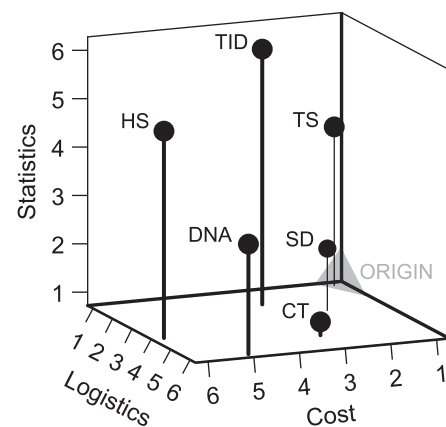


Figure 3. Candidate method ranks plotted by criterion (logistics, statistics, cost) used in method comparison. Ranks range from 1 (best) to 6 (worst). Methods plotted close to the origin are superior to methods far from the origin (TS: track survey, SD: scent dogs, CT: camera traps, DNA: DNA collection, TID: track ID, HS: hair snares).

the value camera traps can have when used for future studies. However, constraints remain on how large an area can be effectively surveyed using camera traps, forcing consideration of alternative approaches (Karanth et al. 2011b).

The remaining three methods proved problematic for various reasons. For DNA collection, variability in sample collection effort limited its effectiveness and collaboration with local laboratories could not be established. Although surveys dependent on outside genetic analyses have been successfully done in the RFE (Sugimoto et al. 2012), recommending a method dependent on outside experts ignores the advantages conferred when conservation infrastructure is self-reliant. Recent development of suitable laboratories in-country increases feasibility for this method (Sorokin et al. 2015), although sample size was still greater using camera traps than DNA collection over the course of our study (Table 2). Hair snares were unsuitable due to small sample sizes. Finally, the track ID method was weakest in terms of sample size. Given the scarcity of suitable substrates for tracks in summer, the tendency of tigers to place hind paws on tracks of front paws in deep snow, and snow condition variability (depth, texture, sublimation rate) acquiring sufficient sample sizes is unlikely in Russia.

Based on our results and subsequent work, track surveys remain the most effective logistically and financially, especially for large areas, while camera traps offer a statistically robust option year-round. Ultimately there is a tradeoff: ease of data collection versus confidence in abundance estimates. Neither track surveys nor camera traps are strong for all criteria desirable in a sampling approach. Because threats are increasing across tiger range, abundance estimates must be as accurate as possible and cover large geographic areas. A double sampling scheme including camera traps and track surveys could allow monitoring across a broad geographic area while incorporating information from a more statistically robust method. Camera traps are more accurate in smaller study areas, but are logistically constrained, forcing consideration of track sign over large landscapes. Double sampling using camera traps and sign surveys to monitor tigers at the landscape scale has been implemented in India (Jhala et al. 2011). However, the value of such an approach has been questioned, particularly when probability of detecting an individual on any given sampling occasion is variable or not very high (Gopalaswamy et al. 2015). Occupancy sampling has been employed for elusive carnivores across broad areas (Karanth et al. 2011b) but this approach does not provide estimates of abundance and may not adequately track changes in abundance, particularly for a carnivore with large, flexible home ranges. While some may argue that occupancy patterns may be sufficient for population monitoring, nearly all government agencies are pressured to report absolute abundance. Combining different sources of information to increase precision is likely a way forward (Gopalaswamy et al. 2012).

In the end, biologists and managers must determine what monitoring scheme is most appropriate for Amur tigers given conservation goals, but consideration of the logistical and cost constraints of each method should be included alongside consideration of statistical robustness. While species occurring over limited areas are suited to intensive methods that provide the most robust abundance estimates, these

methods are rarely feasible to apply over areas of sufficient size to monitor Amur tigers. Proponents of the most statistically rigorous sampling methods may take exception to our focus on logistics and cost. However, in parts of the world where wildlife management funding competes closely with issues of human health and poverty, cost limitations of a method become significantly important. Failure to consider these limitations may doom the long-term implementation of a statistically superior approach. Employing a rubric to compare the relative logistical, statistical and cost constraints of candidate methods provides managers and statisticians an objective means of evaluating monitoring options and facilitates consideration of important limitations.

Acknowledgements – We thank A. A. Astafiev and M. N. Gromyko of Sikhote-Alin Zapovednik, the Wildlife Conservation Society, and the University of Wyoming for logistical and administrative support. We appreciate the assistance of local technicians, scientists and forest guards who helped collect field data. We thank Taro Sugimoto for sharing data from his work in Southwest Primorye.

Funding – Financial support for this project was provided by Rufford Small Grants, the US Forest Service International Programs, Global Forest, the Oregon Zoo, Kaplan Awards, Liz Claiborne and Art Ortenburg Foundation, and the Wildlife Conservation Society. Additional support was provided by Idea Wild, Calvin Klein and Four Paws.

References

- Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. – *Wildl. Soc. Bull.* 29: 1294–1297.
- Becker, E. F. 1991. A terrestrial furbearer estimator based on probability sampling. – *J. Wildl. Manage.* 55: 730–737.
- Belant, J. L. et al. 2005. American black bear population size and genetic diversity at Apostle Islands National Lakeshore. – *Ursus* 16: 85–92.
- Carroll, C. and Miquelle, D. G. 2006. Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: the role of protected areas and landscape matrix in population persistence. – *J. Appl. Ecol.* 43: 1056–1068.
- Efford, M. G. 2004. Density estimation in live-trapping studies. – *Oikos* 106: 598–610.
- Efford, M. G. 2016. *secr*: Spatially explicit capture–recapture models. – R package ver. 2.10.3 (<<http://CRAN.R-project.org/package=secr>>).
- Gompper, M. E. et al. 2006. A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. – *Wildl. Soc. Bull.* 34: 1142–1151.
- Goodrich, J. M. et al. 2010. Spatial structure of Amur (Siberian) tigers (*Panthera tigris altaica*) on Sikhote-Alin Biosphere Zapovednik, Russia. – *J. Mammal.* 91: 737–748.
- Gopalaswamy, A. M. et al. 2012. Density estimation in tiger populations: combining information for strong inference. – *Ecology* 93: 1741–1751.
- Gopalaswamy, A. M. et al. 2015. An examination of index-calibration experiments: counting tigers at macroecological scales. – *Meth. Ecol. Evol.* 6: 1055–1066.
- Groves, G. R. et al. 2002. Planning for biodiversity conservation: putting conservation science into practice. – *BioScience* 52: 499–512.
- Hayward, G. D. et al. 2002. Monitoring Amur tiger populations: characteristics of track surveys in snow. – *Wildl. Soc. Bull.* 30: 1150–1159.

- Jhala, Y. et al. 2011. Can the abundance of tigers be assessed from their signs? – *J. Appl. Ecol.* 48: 14–24.
- Karanth, K. U. and Nichols, J. D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. – *Ecology* 79: 2852–2862.
- Karanth, K. U. et al. 2002. Field surveys: estimating absolute densities of tigers using capture–recapture sampling. – In: Karanth, K. U. and Nichols, J. D. (eds), *Monitoring tigers and their prey: a manual for researchers, managers, and conservationists in tropical Asia*. Centre for Wildlife Studies, Bangalore, India, pp. 139–152.
- Karanth, K. U. et al. 2011a. Estimating tiger abundance from camera trap data: field surveys and analytical issues. – Springer.
- Karanth, K. U. et al. 2011b. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. – *J. Appl. Ecol.* 48: 1048–1056.
- Kerley, L. L. and Salkina, G. P. 2007. Using scent-matching dogs to identify individual Amur tigers from scats. – *J. Wildl. Manage.* 71: 1350–1356.
- Kucherenko, S. 2001. Amur tiger between centuries. – *Okhota i okhotnichye khozyaistvo (Hunting and hunting economy)* 4: 20–24.
- MacKenzie, D. I. et al. 2005. Improving inferences in population studies of rare species that are detected imperfectly. – *Ecology* 86: 1101–1113.
- Matyushkin, E. N. 1977. The choice of route and territory used by the Amur tiger (according to winter tracking data). *Povedenie mlekopitaiuschikh. Voprosy teriologii. M.* – Nauka 146–178 in Russian.
- McDaniel, G. W. et al. 2000. Efficacy of lures and hair snares to detect lynx. – *Wildl. Soc. Bull.* 28: 119–123.
- McKelvey, K. S. et al. 2006. DNA analysis of hair and scat collected along snow tracks to document the presence of Canada lynx. – *Wildl. Soc. Bull.* 34: 451–455.
- Miquelle, D. G. et al. 1999. Hierarchical spatial analysis of Amur tiger relationships to habitat and prey. – In: Seidensticker, J. et al. (eds), *Riding the tiger: tiger conservation in human-dominated landscapes*. Cambridge Univ. Press, pp. 71–99.
- Miquelle, D. G. et al. 2006. A theoretical basis for surveys of Amur tigers and their prey base in the Russian Far East. – *DalNauka, Vladivostok, Russia*, in Russian.
- Miquelle, D. G. et al. 2010. Science-based conservation of Amur tigers in Russian Far East and northeast China. – In: Tilson, R. and Nyhus, P. (eds), *Tigers of the world: the science, politics and conservation of *Panthera tigris**, 2nd edn. Elsevier, pp. 339–419.
- Miquelle, D. G. et al. 2015. Population dynamics of Amur tigers (*Panthera tigris altaica*) in Sikhote-Alin Biosphere Zapovednik: 1966–2012. – *Integr. Zool.* 10: 315–328.
- Mondol, S. et al. 2009. Evaluation of non-invasive genetic sampling methods for estimating tiger population size. – *Biol. Conserv.* 142: 2350–2360.
- Otis, D. L. et al. 1978. Statistical inference from capture data on closed animal populations. – *Wildl. Monogr.* 62: 1–135.
- Pledger, S. 2000. Unified maximum likelihood estimates for closed capture–recapture models using mixtures. – *Biometrics* 56: 434–442.
- Protas, Y. L. et al. 2010. Characteristics of marking activity of the Amur tiger. Paper presented at the The Amur tiger in Northeast Asia: planning for the 21st Century, Vladivostok.
- Robinson, H. S. et al. 2015. Mortality of Amur tigers: the more things change, the more they stay the same. – *Integr. Zool.* 10: 344–353.
- Royle, J. A. et al. 2009. Bayesian inference in camera-trapping studies for a class of spatial capture–recapture models. – *Ecology* 90: 3233–3244.
- Sharma, S. et al. 2005. Identification of individual tigers (*Panthera tigris*) from their pugmarks. – *J. Zool.* 267: 9–18.
- Sorokin, P. A. et al. 2015. Genetic structure of the Amur tiger (*Panthera tigris altaica*, Timminck 1884) population: are tigers in sikhote-alin and southwest primorye truly isolated? – *Integr. Zool.* 10: 25–32.
- Soutyrina, S. V. et al. 2013. A population estimate of Amur tigers using camera traps. – *DalNauka, Vladivostok*.
- Stephens, P. A. et al. 2006. Estimating population density from indirect sign: track counts and the Formozov–Malyshev–Perelshin formula. – *Anim. Conserv.* 9: 339–348.
- Sugimoto, T. et al. 2012. Population size estimation of Amur tigers in Russian Far East using noninvasive genetic samples. – *J. Mammal.* 93: 93–101.
- Weaver, J. L. et al. 2005. Use of scented hair snares to detect ocelots. – *Wildl. Soc. Bull.* 33: 1384–1391.
- Wilson, G. J. and Delahay, R. J. 2001. A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. – *Wildl. Res.* 28: 151–164.

Supplementary material (available online as Appendix wlb-00253 at <www.wildlifebiology.org/appendix/wlb-00253>). Appendix 1.