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Transboundary cooperation improves endangered species monitoring and conservation actions: A case study of the global population of Amur leopards

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Abstract
Political borders and natural boundaries of wildlife populations seldom coincide, often to the detriment of conservation objectives. Transnational monitoring of endangered carnivores is rare, but is necessary for accurate population monitoring and coordinated conservation policies. We investigate the benefits of collaboratively monitoring the abundance and survival of the critically endangered Amur leopard, which occurs as a single transboundary population across China and Russia. Country-specific results overestimated abundance and were generally less precise compared to integrated monitoring estimates; the global population was similar in both years: 84 (70–108, 95% confidence interval). Uncertainty in country-specific annual survival estimates were approximately twice the integrated estimates of 0.82 (0.69–0.91, 95% confidence limits). This collaborative effort provided a better understanding of Amur leopard population dynamics, represented a first step in building trust, and lead to cooperative agreements to coordinate conservation policies.

KEYWORDS
Amur leopard, camera traps, carnivore, China, mark-recapture, monitoring, Panthera pardus orientalis, Russia, transboundary conservation

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INTRODUCTION

Political borders and natural boundaries of wildlife populations seldom coincide, often to the detriment of conservation objectives. The impact of divided and uncoordinated monitoring and management of wildlife populations along political borders has recently received substantial attention (Bischof, Brøseth, & Gimenez, 2016; Ellison, 2014; Gervasi et al., 2016; Lambertiucci et al., 2014; Linnell & Boitani, 2012; Linnell et al., 2016). Growing awareness of this problem has also led to the recognition that border regions retain some of the best habitat for remnant populations of rare and endangered wildlife due to restricted public access (e.g., Sanderson et al., 2006).

Construction of border fences can divide populations, disrupt migrations or individual movements, and eliminate genetic exchange, ultimately reducing population size and viability (Linnell et al., 2016). Even without barriers, animals that travel across political boundaries are usually subject to different management regimes on each side of the border, with most management decisions being made within countries, and often even more locally (Gervasi et al., 2016; Linnell et al., 2016). For large carnivores and other species that move long distances and have large home ranges, transboundary populations are subject to two or more management regimes with unclear consequences. This mismatch between the scale of the ecological processes for large carnivores and the scale of their management and monitoring systems can obfuscate trends and dynamics of these populations (Gervasi et al., 2016), greatly hindering decision-making processes.

Even simple transboundary exchange of basic monitoring information is often difficult due to language barriers, mistrust, differences in sampling designs, and varying collection protocols. Despite these difficulties, sharing data can improve accuracy and precision, and will nearly always provide a better understanding of the status of wildlife populations than assessments done separately (Bischof et al., 2016; Gervasi et al., 2016).

Amur, or Far Eastern leopards (Panthera pardus orientalis, Schlegel, 1857) are designated as Critically Endangered on the IUCN Red List (Stein et al., 2016) and are perhaps the most endangered large carnivores in the world (Platt, 2013). They historically ranged throughout much of northeast China (Yang et al., 2016) and the Korean peninsula (Nowell & Jackson, 1996) with their northern limits reaching southern Primorskii Province of Russia (Heptner & Sludskii, 1992). Since the 1970s, a single population of Amur leopards has been isolated in southwest Primorsky Province (Hebblewhite, Miquelle, Aramilev, & Pikunov, 2011; Pikunov, 2010) with individuals filtering across the border into Jilin Province, China (Yang et al., 1998; Figure 1). More recent evidence suggests a recovery of Amur leopards is occurring in China along the Russian border (Feng et al., 2017, Wang, Feng, Mou et al., 2016; Wang, Feng, Yang et al., 2016). With no evidence of Amur leopards occurring elsewhere (Heptner & Sludskii, 1992), this single transboundary population represents the global population of this subspecies.

We use the transboundary population of Amur leopards to empirically evaluate the consequences of monitoring a population of a wide-ranging endangered carnivore via disjoint country-specific programs. We specifically estimate annual abundance and survival, two important demographic parameters commonly used in making conservation decisions. We also investigate within and between year movements of individual leopards between China and Russia, as movement is a fundamental process that affects the estimation of both abundance and survival and also can clarify the level of mixing of individuals throughout the region. There are few estimates of leopard survival rates across their range (Balme, Slotow, & Hunter, 2009; Swanepoel et al., 2015), but given that recovery is in the early stages in China, while available habitat in Russia appears to be fully occupied, we suspected that survival rates between the two countries may differ. Our objectives are to (a) use a combined photographic-sampling data set to document the extent individual leopards use Russia and China; (b) estimate annual abundance, density, and survival of leopards using a combined data set for China and Russia; and, (c) compare the accuracy and precision of combined estimates to the same parameters for China and Russia separately using country-specific data. We discuss the importance of our findings for monitoring and conserving endangered transboundary populations and demonstrate how transnational monitoring helped build greater cooperation and coordination of conservation policies for this transboundary landscape.

METHODS

Available/Protected habitat and past surveys

Track surveys suggest that nearly all available habitat in southwest Primorye Province of Russia is inhabited by leopards (Hebblewhite et al., 2011; Pikunov, 2010), and most is protected by Land of the Leopard National Park (LLNP). Most leopards on the Chinese side occur in Hunchun National Nature Reserve, but beyond its boundaries extensive habitat in China remains with few leopards (Wang, Feng, Mou et al., 2016; Wang, Feng, Yang et al., 2016). The border in this region (Figure 1) is mostly unfenced except close to a few Chinese villages, but a Russian barbed-wire “border” fence exists between 200 and 10,000 m from the actual national border. Camera trap monitoring indicates that leopards regularly cross the Russian fence (Vitkalova & Shevtsova, 2016).

Camera trapping to estimate Amur leopard abundance began in 2003 in southwest Primorye, but due to logistical and
technical constraints, only a small portion of suitable leop-
ard habitat was consistently surveyed (Aramilev et al., 2010). Starting in 2013, extensive but independent camera-trap mon-
itoring programs were established in Russia and China to
detect leopards throughout most of their known habitat (Feng
et al., 2017; Vitkalova & Shevtsova, 2016; Wang, Feng, Mou
et al., 2016). Subsequent exchanges between countries led to a
formal agreement to combine data and develop robust global
population models to estimate key demographic parameters.

2.2 | Photographic-Sampling and analyses

We sampled leopards across their known distribution in
China and Russia in 2014 and 2015. In China, camera traps
were placed at locations (441 in 2014, 456 in 2015) aver-
aging 1.88 km apart across a minimum convex polygon of
8,398 km² (Figure 1). At half of these locations, cameras
were placed in pairs to photograph both sides of a passing
animal, while one camera was placed at other sites. In Rus-
sia, pairs of cameras (144 in 2014, 165 in 2015) were spaced,
on average, 4.74 km apart, across 3,071 km². Both layouts
ensured all individual leopards had some chance of being pho-
tographed. Cameras were mostly deployed along forest roads,
ridgelines, and trails commonly used by leopards to maximize
the chances of detection (Supporting Information).

We selected a survey period (90 days) to balance the need
of meeting population closure assumptions with the need
to obtain sufficient recaptures for robust capture–recapture
models (Alexander, Gopalaswamy, Shi, Riordan, & Margal-
ida, 2015; Karanth & Nichols, 1998). Surveys were initiated
in late winter and ended in late spring, coinciding with a
period of high capture rates and slightly warmer tempera-
tures (in extreme cold camera traps do not always function).
Camera trap models used in China were Ltl-6210 M from
Zhuhai Ltl Acron Electronics Co. Ltd (Guangdong, China),
while ScoutGuard (Molendinar, Australia), Bushnell (Over-
land Park, KS), and Reconyx (Holmen, WI) cameras were
deployed in Russia.

Two independent observers used the program Extract/
Compare (Hiby et al., 2009) and their own judgments to iden-
tify individual leopards based on their unique spot patterns
(see Supporting Information). When possible, we identified
sex (usually based on presence/absence of testicles). Although
we report records of cubs photographed, they were excluded
from analyses due to low capture probabilities (Karanth &
Nichols, 1998) and a focus on the mature, reproductive seg-
ment of the leopard population.

We estimated annual survival of the total transbound-
ary population of Amur leopards and for each country-
specific data set using Pollock's robust capture–recapture
model framework (Kendall, Nichols, & Hines, 1997). We con-
sidered models with detection probability as constant or vary-
ing by year, sex, and individual heterogeneity using a random
effect (White & Cooch, 2017), or individual heterogeneity
where the mean and/or variance of the random effect varied
by sex or year. We fit the same eight models to the country-
specific data sets (Russia only, China only) and the combined
two-country data set (Russia & China); we included addi-
tional models for the combined data set analysis that evaluated
country-specific effects on survival and detection.
We estimated annual density and abundance of Amur leopards using a spatially explicit capture–recapture (SECR) modeling approach (Borchers & Efford, 2008). We fit the spatial capture–recapture data using a likelihood approach in the R package “secr” (Efford, 2016). The process model specifically defines density as the number of activity centers in a specified area that extends beyond the trapping area; activity centers are unobserved and estimated from the data (see Supporting Information). Leopards were designated as primarily living in China or Russia based on the location of the most probable estimated activity center. For the Russia and China data sets, we considered ecological hypotheses of whether leopard density (D) varied temporally by year, and whether detection parameters \((g_0, \sigma)\) varied by sex. For the combined two-country data set, we also considered whether leopard density varied by country. For survival, density, and abundance, we used Akaike’s information criterion with a small sample correction to rank models (Burnham & Anderson, 2003) and model-averaged parameter estimates to include model selection uncertainty (for more details on methods, see Supporting Information).

3 | RESULTS

We sampled 51,019 trap nights in 2014 and 53,491 in 2015 (Supporting Information Table S1). Trap effort was two to three times higher on the Chinese side of the border, but capture rates were seven to eight times greater on the Russian side (Supporting Information Table S1). Over both years, 32 adult males, 43 adult females, 13 cubs, and four individuals of unknown sex were photographed (Table 1 and Supporting Information). We observed extensive movement of individual leopards between China and Russia; across both years 38% of all leopards were observed in China but only about half of those (20%) were observed exclusively in China. Nearly 85% of all leopards were observed in Russia, and three-quarters of those were exclusively observed in Russia.

We found differences in point estimates and precision of annual survival of Amur leopards, depending on whether country-specific or combined data were used (Table 2). Survival probabilities of leopards in China and Russia were similar using country-specific data sets, but much lower in Russia than China with the combined data set (Table 2). Using the combined data led to a much higher survival for leopards designated as living in China because three individuals that had only been detected in China in 2014 were then subsequently (2015) only observed in Russia. Thus, the combined data was able to reduce the negative biases of permanent emigration. The combined survival estimates were also more precise: the coefficient of variation (SE/maximum likelihood estimates) for separate China and Russia survival was 0.18 and 0.10, respectively, but dropped to 0.08 and 0.05 for the combined data set. Model selection results indicated detection probability greater for males than females, with stronger evidence coming from the combined data set (for details on model results, see Supporting Information Table S2).

The SECR model results indicated that, in comparison to the combined data set, the China-only data set considerably overestimated leopard density and abundance, but density/abundance estimates using the Russia-only data set were mostly consistent with the global data set (Tables 3 and 4). The combined data set supported evidence for temporal stability in density and abundance for both countries over the two years (see Supporting Information Table S3). We also found that precision was somewhat improved for the Russian density estimate when the combined data set was used, but markedly improved for estimates in China (Tables 3 and 4).

Spatially explicit estimates of Amur leopard abundance in China were much lower when the combined data set was used versus the China-only data set (Table 4), reflecting the fact that many leopards captured in China had activity centers in Russia. The SECR modeling effort suggested there was no difference in the global population estimate between years for the Russia-only and the combined data sets (Supporting Information Table S3). The global spatially explicit population estimate over both years was 84 (70–108, 95% confidence interval; Table 4). Adding the country-specific abundance estimates, thus ignoring individual movement across the border, overestimated abundance compared to the combined analyses by 18%. For all models, the combined data set greatly increased precision.

4 | DISCUSSION

With heightened concern over the status of leopards worldwide (Jacobson et al., 2016), these first robust global abundance and survival estimates for one of the most endangered of leopard subspecies are particularly important. Results provide empirical evidence of the potential biases in estimating demographic parameters when bordering countries do not share data. Despite differences in density and layout of camera traps between Russia and China, the combined data set estimated the global population of Amur leopards with much higher precision than country-specific data sets. Simply adding results of country-specific estimates overestimated Amur leopard abundance by approximately 18%, and greatly reduced precision of key demographic parameters. Our results support the observation of Bischof et al. (2016) that overestimates of carnivore populations along international boundaries were likely without collaboration, and the conclusion of Gervasi et al. (2016) that precision can be greatly increased with collaboration.

Estimating abundance of large carnivores with high precision is notoriously difficult given their often secretive nature,
### Table 1
Numbers and sex of Amur leopards captured in China, Russia, and both countries combined in camera trap surveys in 2014 and 2015

<table>
<thead>
<tr>
<th>Year</th>
<th>Location captured</th>
<th>Females</th>
<th>Males</th>
<th>Cubs</th>
<th>Unknown sex</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>2014</td>
<td>China</td>
<td>14</td>
<td>11</td>
<td>2</td>
<td>0</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>Russia</td>
<td>25</td>
<td>21</td>
<td>3</td>
<td>2</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>China &amp; Russia</td>
<td>33</td>
<td>24</td>
<td>5</td>
<td>2</td>
<td>64</td>
</tr>
<tr>
<td>2015</td>
<td>China</td>
<td>10</td>
<td>12</td>
<td>0</td>
<td>0</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Russia</td>
<td>24</td>
<td>20</td>
<td>8</td>
<td>3</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>China &amp; Russia</td>
<td>31</td>
<td>25</td>
<td>8</td>
<td>3</td>
<td>67</td>
</tr>
<tr>
<td>Total</td>
<td>China</td>
<td>18</td>
<td>15</td>
<td>2</td>
<td>0</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>Russia</td>
<td>35</td>
<td>28</td>
<td>11</td>
<td>4</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>China &amp; Russia</td>
<td>43</td>
<td>32</td>
<td>13</td>
<td>4</td>
<td>92</td>
</tr>
</tbody>
</table>

*Where China and Russia totals exceed China & Russia, it is because some individuals were observed in both countries.*

### Table 2
Model-averaged annual survival estimates from 2014 to 2015 of Amur leopards in China and Russia with country-specific data, and results for each country using the combined data set

<table>
<thead>
<tr>
<th>Data set</th>
<th>Inference</th>
<th>Annual survival</th>
<th>SE</th>
<th>95% Lower confidence limit</th>
<th>95% Upper confidence limit</th>
</tr>
</thead>
<tbody>
<tr>
<td>China-only</td>
<td>China population</td>
<td>0.83</td>
<td>0.15</td>
<td>0.38</td>
<td>0.98</td>
</tr>
<tr>
<td>Russia-only</td>
<td>Russia population</td>
<td>0.87</td>
<td>0.09</td>
<td>0.59</td>
<td>0.97</td>
</tr>
<tr>
<td>China &amp; Russia</td>
<td>Russia population</td>
<td>0.77</td>
<td>0.06</td>
<td>0.62</td>
<td>0.87</td>
</tr>
<tr>
<td>China &amp; Russia</td>
<td>China population</td>
<td>0.99</td>
<td>0.04</td>
<td>0.72</td>
<td>1.00</td>
</tr>
</tbody>
</table>

### Table 3
Model-averaged spatially explicit capture–recapture estimates of Amur leopard density in China and Russia, averaged across both years for the combined data sets and for each year separately for the country-specific data sets. Included are density estimates (individuals/100 km²), SE, and 95% confidence intervals

<table>
<thead>
<tr>
<th>Data</th>
<th>Year</th>
<th>Inference</th>
<th>Density (individuals/100 km²)</th>
<th>SE</th>
<th>95% Lower confidence limit</th>
<th>95% Upper confidence limit</th>
</tr>
</thead>
<tbody>
<tr>
<td>China-only</td>
<td>2014</td>
<td>China population</td>
<td>0.4</td>
<td>0.07</td>
<td>0.29</td>
<td>0.55</td>
</tr>
<tr>
<td>China-only</td>
<td>2015</td>
<td>China population</td>
<td>0.38</td>
<td>0.07</td>
<td>0.27</td>
<td>0.54</td>
</tr>
<tr>
<td>Russia-only</td>
<td>2014</td>
<td>Russia population</td>
<td>1.35</td>
<td>0.16</td>
<td>1.06</td>
<td>1.71</td>
</tr>
<tr>
<td>Russia-only</td>
<td>2015</td>
<td>Russia population</td>
<td>1.34</td>
<td>0.15</td>
<td>1.07</td>
<td>1.68</td>
</tr>
<tr>
<td>Russia &amp; China</td>
<td>2014 &amp; 2015</td>
<td>Russia population</td>
<td>1.4</td>
<td>0.14</td>
<td>1.15</td>
<td>1.7</td>
</tr>
<tr>
<td>Russia &amp; China</td>
<td>2014 &amp; 2015</td>
<td>China population</td>
<td>0.16</td>
<td>0.04</td>
<td>0.08</td>
<td>0.26</td>
</tr>
</tbody>
</table>

### Table 4
Model-averaged spatially explicit capture-recapture abundance estimates of Amur leopards by country and data set

<table>
<thead>
<tr>
<th>Data set</th>
<th>Inference</th>
<th>Year</th>
<th>Abundance</th>
<th>SE</th>
<th>95% Lower confidence limit</th>
<th>95% Upper confidence limit</th>
</tr>
</thead>
<tbody>
<tr>
<td>China-only</td>
<td>China population</td>
<td>2014</td>
<td>31</td>
<td>2.7</td>
<td>27.6</td>
<td>38.8</td>
</tr>
<tr>
<td>China-only</td>
<td>China population</td>
<td>2015</td>
<td>27</td>
<td>2.4</td>
<td>23.9</td>
<td>34.1</td>
</tr>
<tr>
<td>Russia-only</td>
<td>Russia population</td>
<td>2014 &amp; 2015</td>
<td>72</td>
<td>7.9</td>
<td>57.8</td>
<td>89.0</td>
</tr>
<tr>
<td>China &amp; Russia</td>
<td>Global population</td>
<td>(adding China and Russia separate estimates)</td>
<td>2014</td>
<td>103</td>
<td>10.6</td>
<td>85.4</td>
</tr>
<tr>
<td>China &amp; Russia</td>
<td>Global population</td>
<td>(adding China and Russia separate estimates)</td>
<td>2015</td>
<td>99</td>
<td>10.3</td>
<td>81.7</td>
</tr>
<tr>
<td>China &amp; Russia</td>
<td>Russia population</td>
<td>2014 &amp; 2015</td>
<td>73</td>
<td>7.6</td>
<td>63.2</td>
<td>92.3</td>
</tr>
<tr>
<td>China &amp; Russia</td>
<td>China population</td>
<td>2014 &amp; 2015</td>
<td>11</td>
<td>2.4</td>
<td>6.5</td>
<td>16.4</td>
</tr>
<tr>
<td>China &amp; Russia</td>
<td>Global population</td>
<td>2014 &amp; 2015</td>
<td>84</td>
<td>7.9</td>
<td>69.7</td>
<td>108.1</td>
</tr>
</tbody>
</table>
low densities, and, with increasing habitat fragmentation and small population sizes. Reliance on a data-driven decision-making process to define conservation priorities is greatly hindered when precision is low, and trends uncertain. Use of camera traps has greatly increased our ability to accurately estimate population abundance, but precision is nonetheless often low. For populations that cross international boundaries, the added problem of coordinating and cooperating in data collection and analysis makes the process of deriving meaningful population estimates all the more difficult. These results suggest that increased accuracy and precision derived from collaboration makes the effort worthwhile.

These results are congruent with the observation that recovery of leopards is just beginning in China (Wang, Feng, Mou et al., 2016), with distribution still spotty, overall numbers low, but with survival estimates higher than in Russia. We predict that as recovery continues, not only will numbers and density increase in China, but precision of those estimates will also increase as sample sizes increase. Continued collaboration in data analysis will provide a better vehicle to detect such trends, and will provide strong support for maintaining a border that allows free movement of wildlife.

Given the absence of a continuous border fence, it was not surprising that leopards moved across the international border. However, the extent of movement was unexpected. Approximately 20% of all leopards were photographed both in Russia and China, indicating extensive transboundary movement and a need to protect existing habitat continuity along this international boundary.

Given the raised concern and bolstered protection for leopards recently provided under the United Nations Convention on the Conservation of Migratory Species (Cannon, 2017), deriving an accurate estimate of the global population of Amur leopards represents an important baseline to guide conservation action. Previous expert assessments based on track abundance and distribution suggested there may have been only 25 to 34 Amur leopards left in the wild (Pikunov, 2010), prompting efforts to develop a reintroduction program in Russia (Miquelle et al., 2010). Our results suggest the population is larger than expected, but nonetheless given the genetic impoverishment of this subspecies (Sugimoto et al., 2014; Uphyrkina, Miquelle, Quigley, Driscoll, & O’Brien, 2002), this single population is still challenged due to its small size and susceptibility to stochastic events, including disease (Sulikhan et al., 2018). Therefore, reintroduction of a second population remains a priority. At the same time, continued expansion of this single population is desperately needed. On the Chinese side, the government’s recent commitment to a large national park along this border (Feng et al., 2017; Mclaughlin, 2016) gives hope for expansion of both tiger and leopard populations. On the Russian side, improvements in law enforcement efforts (Hötte et al., 2015) provide hope that prey and leopard numbers could still increase within LLNP.

Expansion of the population is also possible on the Russian side if connectivity via an ecological corridor to the Sikhote-Alin Mountains was secured (Miquelle et al., 2015). This first ever global population estimate has spurred discussions both within and between governments to prioritize expansion of this remaining population (T. Baranovskaya, 2017, personal communication).

Recovering extremely small populations requires precise and accurate monitoring (Setiawan et al., 2017). This joint effort, which increased both precision and accuracy, was successful largely because biologists and administrators from governments, universities, and NGOs committed to the effort, and recognized the value of collaboration. A coordinated monitoring program is evolving out of this effort, a two-way agreement was signed by heads of the key protected areas in China and Russia, and there now exists a joint working group that represents the start of coordinated transboundary management of this landscape—a rarity anywhere in the world (Linnell & Boitani, 2012). This survey acted as the first step in building trust and collaboration, and will hopefully lead to creation of a transboundary biosphere reserve, resulting in coordinated management and protection not just for leopards, but for ensuring the integrity of the ecosystem and the persistence of all species inhabiting this landscape.

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REFERENCES


SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section at the end of the article.