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'I know the tiger by his paw': A non-invasive footprint identification technique for monitoring individual Amur tigers (*Panthera tigris altaica*) in snow

Sky K. Alibhai[a,b,1], Jiayin Gu[c,1], Zoe C. Jewell[a,b,*], Joseph Morgan[b], Dan Liu[d], Guangshun Jiang[c,**]

[a] *Nicholas School of the Environment, Duke University, Box 90329, Durham, NC 27708, USA*
[b] *SAS Institute Inc., JMP Division, SAS Campus Drive, Cary, NC 27513, United States of America*
[c] *Feline Research Center of National Forestry and Grassland Administration, College of Wildlife and Protected Area, Northeast Forestry University, Harbin 150040, PR China*
[d] *Heilongjiang Siberia Tiger Park, Harbin, Heilongjiang, 150028, China*

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ABSTRACT

Apex predator populations are in decline around the world. Many exist at low density and are elusive, making the acquisition of reliable data on their numbers and distribution a considerable challenge. The Amur tiger (*Panthera tigris altaica)* is the largest of the five extant sub-species of tiger. The single most significant, contiguous population, an estimated 550 animals, exists in the Russian Far East, with smaller populations on the far eastern Sino-Russian border. For the last few decades, active efforts on the part of Chinese authorities have encouraged the recolonization of these populations back to their former ranges in Northeast China. Reliable data on Amur tiger numbers and distribution are required to assess population recovery at the landscape scale. Footprints, ubiquitous in the snow over range areas, could inform on these baseline data. This paper describes a statistically robust, cost-effective and non-invasive footprint identification technique (FIT) to identify individual tigers from footprints in snow. It is based on a rigorous data collection and data-processing protocol, combined with a cross-validated discriminant analysis method. A Ward's clustering technique provides a visual output of individual classification. The analytical tools are packaged in a user-friendly analytical interface. Between December 2011 and December 2012, we collected a series of 605 footprint images from 44 captive individual Amur tigers for a reference database from which to derive a classification algorithm. The 23 females and 21 males ranged in age from 3 to 13 years (female mean age 7.95 +/− 0.18; male mean age 8.08 +/− 0.19). 128 measurements (areas, lengths and angles) were taken from each print and analyzed with the FIT add-in to JMP software. The derived classification algorithm was then applied to 21 footprint trails collected from an unknown number of free-ranging Amur tigers during 2012 and 2015/2016. The algorithm predicted 7 Amur tigers at the site surveyed in 2012, and 4 tigers surveyed at two sites in 2015/16. We demonstrate that the footprint identification technique translates traditional tracking methodologies into a statistically robust and objective analytical tool that can be deployed by both scientists and local communities to monitor the recovery of big cat populations.

1. Introduction

Apex predators, such as the big cats, play vital regulatory roles in maintaining healthy ecosystems by exerting top-down pressure on prey communities and their disappearance can cause negative impacts ranging from loss of plant biodiversity, biomass and a loss of productivity, that in turn can change disease dynamics, carbon sequestration and increase wildfire risk (O'Bryan et al., 2018). Big cat populations are declining around the world due to many factors such as the loss of their natural habitat, reduction in prey base, human-wildlife conflict, illegal

* Corresponding author at: Nicholas School of the Environment, Duke University, Box 90329, Durham, NC 27708, USA
** Corresponding author.
E-mail addresses: info@wildtrack.org (Z.C. Jewell), jgshun@126.com (G. Jiang).
[1] Joint first authors

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killing, pollution and climate change (Ordiz et al., 2021).

The endangered Amur tiger (*Panthera tigris altaica*) is the largest subspecies of tiger and is currently distributed primarily in Southeast Russia with small populations in Northeast China on the Sino-Russian and North Korean borders (IUCN, 2021; Qi et al., 2020). Until the 20th century, the species ranged widely across the Russian Far East, the Korean Peninsula and northern China. However, by the 1960s, a combination of habitat degradation and fragmentation, combined with poaching, had reduced the population to an estimated 400 animals in Russia and small contiguous areas of Northeast China (Kerley et al., 2015). By 2000, only 12–16 individuals remained along the Sino-Russian border (Ma and Zhang, 2009).

In the last few decades, Chinese authorities have actively encouraged the Amur tiger back into its historic range in China, beginning with areas on the far eastern side of the Sino-Russian border. In 2016, China created the 14,600 km^2 Northeast Tiger Leopard National Park (NTLNP) in the eastern Laoyeling forests bordering Russia, currently the world's largest protected area for tigers (Qi et al., 2021). This area, and the adjacent Changbaishan Mountains are the primary focus of Amur tiger conservation by the Chinese authorities (McLaughlin, 2016; Northeast Tiger Leopard National Park of China, 2016). Together with the implementation of prey-stocking, this habitat protection has resulted in the population starting to disperse back to its former range in China (Wang et al., 2015; Wang et al., 2018). It has been suggested that China might restore a sustainable meta-population of 310 tigers including 119 resident breeding females into four current major forested landscapes (Qi et al., 2021) where tiger habitat is optimal (Jiang et al., 2014). Regular and effective monitoring is key to the successful recolonization of these areas, since tigers require relatively large populations to persist, are quite susceptible to modest increases in mortality, and are less likely to recover quickly after population declines (Chapron et al., 2008; Rozhnov et al., 2019). Monitoring the numbers and distribution of the Amur tiger presents further challenges, because they exist at very low population densities (Miquelle et al., 2010). The average home range for a female tiger was reported as 390 km^2, and for a male up to 2000 km^2 (MacKenzie et al., 2005).

Several methods have been used to attempt to census and monitor Amur tiger populations. To date, camera-traps (Matyukhina et al., 2016; Wang et al., 2018), microsatellite analysis of DNA extracted from scat (Dou et al., 2016; Ning et al., 2019) and scent-matching dogs (Kerley and Salkina, 2007), have provided most of the available population estimates including the more recent Spatially Explicit Capture-Recapture (SECR) models that permit inclusion of spatial data and avoid the assumption that the population being sample is 'closed'. SECR models are most commonly used for estimating population density in big cats that can be identified from gross morphology e.g. coat pattern (Borchers and Efford, 2008; Royle and Young, 2008; Wang et al., 2018).

Mammal species often leave footprints that are sufficiently distinctive to permit the identification of the sex and individual(s) who made them. There have been many reported attempts to use footprints ranging from reporting footprints as a simple index of abundance (Karanth et al., 2010; Karanth et al., 2011) for occupancy analysis, to taking simple measurements directly from footprints in the field for brown bear *Ursus arctos* (Edwards and Green, 1959; Klein, 1959) and tiger *Panthera tigris* (Panwar, 1979), to visual pattern recognition Fisher, *Martes pennanti* (Herzog et al., 2007) and unsupervised neural nets in Snow leopard, *Panthera uncia,* (Riordan, 1998). More rigorous morphometric approaches have been reported for European pine marten, *Martes martes* (Zalewski, 1999) and tiger, (Panwar, 1979; Riordan, 1998; Sharma et al., 2005). One approach, the Footprint Identification Technique (FIT) has been described for several different species and is based on rigorous data collection protocols, large training data sets and a robust cross-validated discriminant analysis, integrated into a user-friendly analytical software. It has been reported for Black rhinoceros, *Diceros bicornis*, (Jewell et al., 2001); White rhinoceros, *Ceratotherium simum* (Alibhai et al., 2008) *Puma concolor* (Alibhai et al., 2017); cheetah, *Acinonyx jubatus* (Jewell et al., 2016); Lowland tapir, *Tapirus terrestris* (Moreira et al., 2018) and Giant panda, *Ailuropoda melanoleuca* (Li et al., 2018). Examples of three different field applications of FIT were reported by for a closed population of black rhinoceros, based on the requirement for data granularity, frequency of monitoring and availability of local resources using this same technique (Jewell et al., 2020).

The traditional method of identifying individual Amur tigers from footprints in the snow, practiced mainly in the Russian Far East, is based on measurements of the width of the front paw palmar pad that vary with age and sex. It is considered quick, simple, and inexpensive (Hayward et al., 2002). However, challenges remain in discriminating the similarly sized sub-adult males and mature females (Yudakov et al., 2012). The identification of Amur tiger sex from footprints in snow in Northeast China was reported by Gu et al. (2014) using a statistically robust morphometric approach.

FIT is an example of a class of emerging, statistically reliable, non-invasive, and cost-effective techniques, driven by growing concern over invasive approaches (Alibhai et al., 2001; Long et al., 2012; Pimm et al., 2015; Zemanova, 2020), and their risk of invalidating data collected (Jewell, 2013). Footprints are ubiquitous across many big cat habitats, easier to locate than the animals themselves, and, since trails remain sometimes for days, can offer a record of the exact movement patterns of animals as well as their presence/absence and, using FIT, sex and individual identity.

We report here on the development of a FIT algorithm for individual identification of Amur tigers in snow substrates, we apply this identification algorithm to an arbitrary sample set of footprints captured from free-ranging Amur tigers in Northeast China, and we introduce FIT for the Amur tiger as a potentially wider application for big cats in both snow and other substrates.

2. Materials and methods

2.1. Definition of terms

Footprint: An impression made by a foot on a substrate

Trail: An unbroken series of footprints made by a single animal.

Sub-trail: A trail obtained by sub-dividing one long natural trail, into shorter segments.

2.2. The study area

The study areas were chosen based on their ability to provide anecdotal evidence of tiger presence every year (Ning et al., 2019; Zhu et al., 2019) and their potential to support tigers (Li et al., 2016; Zhang et al., 2013). We collected footprints from both captive and free-ranging Amur tigers in three areas of Northeast China; Zhangguangcailing, the Wanda Mountains and the Lesser Khingan Mountains. In these dispersal areas, footprints are the main source of information about Amur tiger presence, especially in winter (Fig. 1).

Footprints from captive Amur tigers were collected from the Hengdaohezi Amur Tiger Breeding Center in the Heilongjiang Province of North-East China, where records are kept on date of birth and parentage for >300 Amur tigers.

2.3. Materials for collection and analysis

Our objective was to develop a classification algorithm in the FIT that would allow identification of individual Amur tiger from their footprints in snow. The classification algorithm was derived from footprints collected from captive Amur tiger of known identity, validated on this dataset, and then applied to footprints collected from free-ranging Amur tiger. The technique is based on the morphometric analysis of sequences of footprints along a trail. We collected images of Amur tiger footprints using a photo protocol described in detail by Gu et al., 2014, with a basic Sony cyber-shot compact digital camera. We used a 20 cm

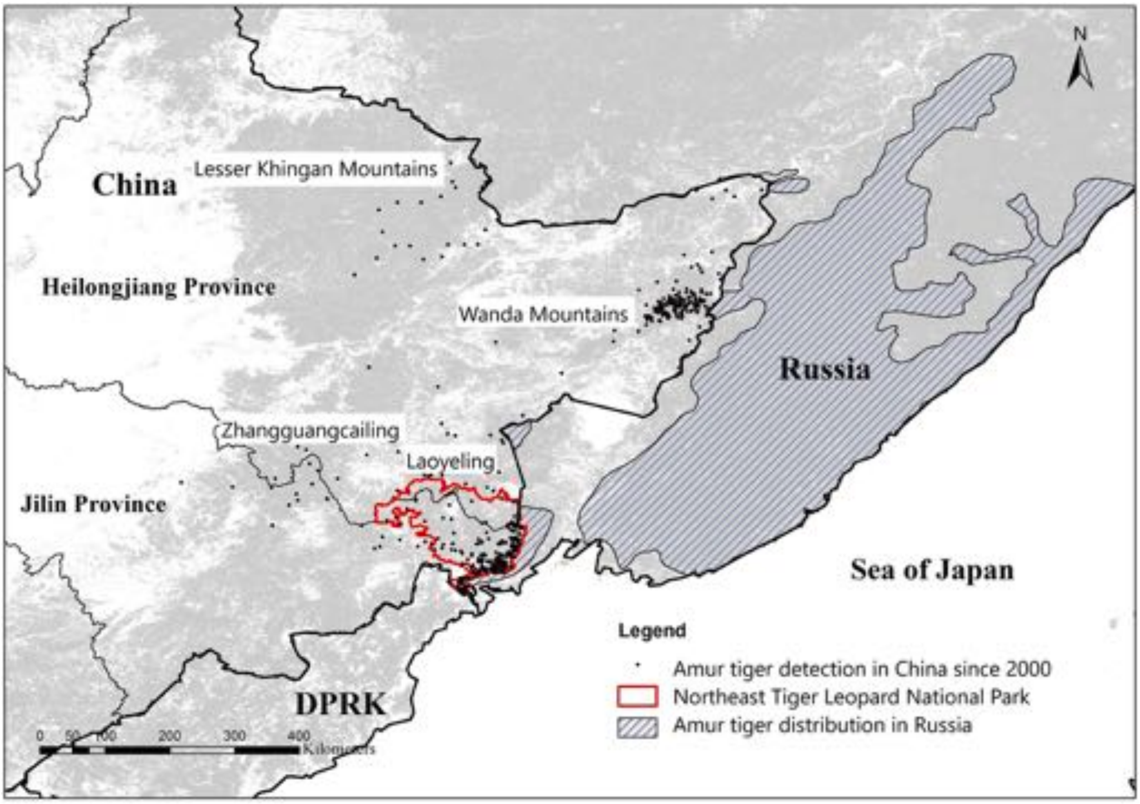

Fig. 1. Areas A (Wanda Mountains), B (Lesser Khingan), & C (Zhangguangcailing) of Amur tiger expansion into China, outside the Northeast Tiger Leopard National Park (NTLNP) where free-ranging Amur tiger footprint trails were detected and photographed in 2012 and 2015/16.

carpenters' metric folding ruler to provide scale. We imaged only those footprints demonstrating clear outlines of the 4 toes and metapodial pad. Fig. 2 provides examples of the different qualities of the footprints. Supplementary Fig. 1 demonstrates the consistency of footprint quality between captive and free-ranging tigers.

2.4. Developing a classification algorithm using footprints from captive Amur tigers

We developed a classification algorithm by extracting measurements from a set of footprints (the training set) collected from 44 captive individuals in a breeding facility, whose records of identity, sex and date of birth were available. Their ages ranged from 3 to 13 years old (both females and males) (Table 1).

Due to an atypical shortage of snow during the sampling period, we augmented the enclosure spaces with natural, sifted snow, laid to 2-3 cm depth, to imitate natural conditions. We encouraged animals, using food rewards, to walk over the surface, then moved them on to a safe enclosure before collecting footprints. Each footprint was photographed to the FIT protocol (Alibhai et al., 2008) placing a metric scale ruler to the left and bottom of the footprint in relation to the direction of travel (See Figs. 3, 2.6 below). Details of the date, name of photographer, location and animal ID (if known) were recorded on a plastic wipe-off strip below the ruler. We collected only left hind footprint images for analysis in this study. Hind feet were used in preference to front feet because they are more accessible in situ in cases where footprint registration (the placing of the hind foot on top of the front footprint) occurs. The FIT requires all prints to be from the same foot, and the left hind footprint was chosen arbitrarily.

Snow substrates typically demonstrated high reflectivity, resulting in low-contrast images. We obtained optimal images by photographing early and late in the day and provided artificial lighting from a flashlight when conditions were overcast and visibility very poor.

2.5. Collection of footprints from free-ranging Amur tigers

In the winters of 2012 and 2015/6 we located and collected multiple high-quality footprints from free-ranging Amur tigers. Images were collected opportunistically when teams were notified of trails by local villagers and patrollers. Despite challenging field conditions, it was not difficult to find clear footprints. The field team was accompanied by local trackers who used their experience to locate footprints on level terrain such as frozen rivers, roads, ridges and farmland. Supplementary fig. 2 demonstrates examples of free-ranging trails in snow. However, when footprints were found in very deep snow, excess snow around the footprint was manually removed to keep the ruler and the outline of the footprint on the same plane. Fresh snowfall, wind, ice overflow, and melt-out caused some footprints to degrade. Fresh snowfall was the most common cause (82%) of footprint degradation in January and February, while footprints created later in the season tended to degrade faster (lasting on average 2.1 days) because of warm weather and wind (Hayward et al., 2002).

While footprints collected from captive tigers were labelled with their individual name, sex and age, we recorded footprints from free-ranging tigers (of unknown identity) as trail identities, in the following manner: the first trail imaged each day was labelled trail 1, and each sequential footprint recorded as 1a, 1b, 1c, etc. The second trail was trail 2, and footprints recorded as 2a, 2b, etc. If a trail was obscured or broken at any point, the next set of images was allocated the next trail number to avoid an assumption of identity. Geo-locations were recorded for each trail, along with habitat information.

2.6. Algorithm development for classification of individual Amur tigers from footprint images

The identification algorithm was derived from footprints collected from captive Amur tiger of known identity. Between December 2011

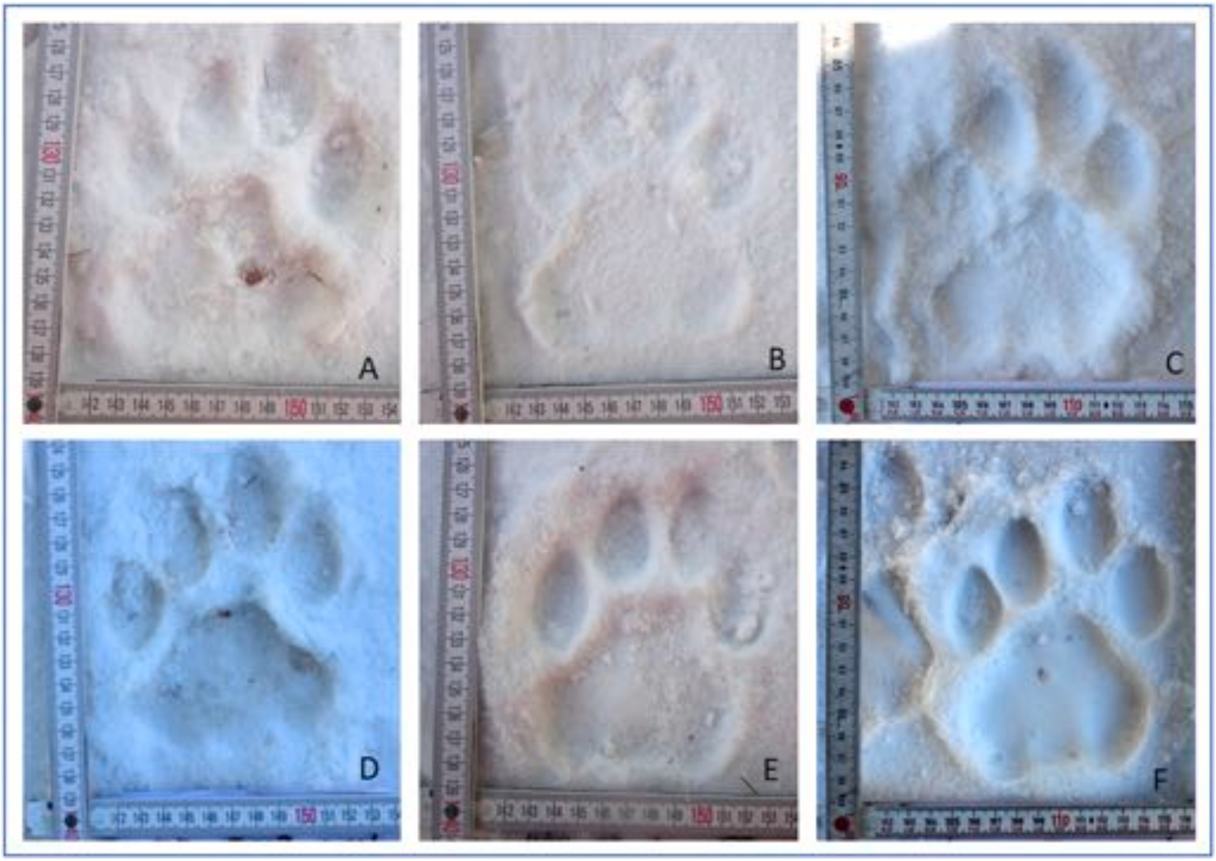

Fig. 2. Images A-C exhibited unclear outlines and were discarded, while images D—F were used for analysis. We maintained the same quality control over prints from both captive and free-ranging tigers.

and December 2012, we collected a series of 605 footprints from 44 captive tigers; the age range for the 23 females and 21 males was 3–13 years (female mean age 7.95 +/− 0.18; male mean age 8.08 +/− 0.19). The process of developing a classification algorithm has been described by Alibhai et al., 2017. Below we summarize the process as it applies to monitoring the Amur tiger in snow.

We imported footprint images into the FIT software feature extraction window in JMP v.16 software (Fig. 3) where a customized script extracted 128 measurable variables, or features, (distances, angles, and areas) of each footprint to provide a comprehensive geometric profile.

Each field image was imported (by simple drag and drop) into the software platform, and then rotated into a standardized orientation using a horizontal axis provided by joining two designated landmark points (points 1 & 13). Twenty-five anatomically defined landmark points were then positioned on the footprint, and from these a further 15 points were derived using a predetermined script. This provided 40 points on each footprint, from which measurements of distances, angles and areas were then automatically extracted, producing a total of 128 variables for analysis. These variables constituted the 'geometric profile' of the footprint.

Table 1 (see 2.4 above) describes the derivation of each measurement (variable).

2.6.1. Sex identification

We deployed a sex classification algorithm based on discriminant analysis, described in detail by Gu et al. (2014), to assign sex to free-ranging tiger footprints as a preliminary classification filter prior to identifying individuals from their trails. We also investigated footprints variable profiles by sex and age-class using the same approach.

2.6.2. The individual identification procedure

The FIT individual classification model is based on a pairwise comparison of each trail with every other trail (Alibhai et al., 2017; Jewell et al., 2016; Li et al., 2018). Pairwise comparisons for known animals will include self trails (where both trails compared are from the same animal) and non-self trails (where each of the two trails is from a different animal). The process involves two sequential steps. First, a cross-validated discriminant analysis is used to determine the distance between the centroid values of pairs of trails, each with a 95% confidence ellipse. Secondly, using the matrix distance from the discriminant analysis step, a Ward's hierarchical clustering method that partitions trails into clusters to minimize within-cluster variance, is used to generate a dendrogram. The predicted number of individuals is determined by the number of clusters estimated by the hierarchical clustering method. The number of clusters is the inflection point of the distance plot of cluster distances that indicates that the difference in clusters beyond that point would be large. This is referred to as the "knee of a curve" method (Salvador and Chan, 2004). To augment the number of available trails, longer trails were arbitrarily divided into sub-trails for both captive and free-ranging populations (Alibhai et al., 2017).

The development of the individual classification algorithm is described in detail in Li et al., 2018. Fundamentally, the process entails the optimization of three features within the FIT model construct: the number of variables in the model, the size of the confidence intervals around the ellipse, and the threshold value of the distances between the means. Algorithm validation was conducted using holdback trials. The dataset of 44 known captive Amur tigers was partitioned sequentially into different ratios of test and training subsets. Using the optimal algorithm generated in FIT, this dataset was iterated 10 times for each random combination of test/training size, to examine how the predicted outcome compared with the known test size. After algorithm validation,

Table 1
The number of variables extracted from the footprint images as lengths (L), angles (A) and areas. The numbers 01–25 refer to the landmark points and 26–40 to points derived from the landmark points by predetermined geometric relationships. For example, variables 81–88 were generated at the intersection of two vectors e.g. V81 refers to the angle formed by the intersection of the vector from points 01 to 05 with the vector from points 09 to 13. Areas were generated using the most peripheral points in each case. Area 1 = whole image, Area 2 = toe 5, Area 3 = toe 4, Area 4 = toe 3, Area 5 = toe 2, Area 6 = pad, Area 7 = points 1, 5, 9 & 13 and the proximal pad points, Area 8 = points 1 & 13 and the proximal pad points, Area 9 = points 1, 5, 9 & 13 and points 19 & 25, Area 10 = points 1 & 13 to the most distal toe points (3,7, 11 & 15).

Variable	Description	Variable	Description	Variable	Description	Variable	Description
V01	L 01–03	V33	L 03–07	V65	L 14–15	V97	L 02–37
V02	L 05–07	V34	L 07–11	V66	L 15–16	V98	L 02–36
V03	L 09–11	V35	L 11–15	V67	L 13–16	V99	L 26–36
V04	L 13–15	V36	L 15–19	V68	L 17–19	V100	L 11–26
V05	L 02–04	V37	L 03–25	V69	L 18–25	V101	L 11–39
V06	L 06–08	V38	L 17–27	V70	L 27–28	V102	L 16–39
V07	L 10–12	V39	L 17–28	V71	L 28–29	V103	L 16–38
V08	L 14–16	V40	L 17–29	V72	L 29–30	V104	L 24–38
V09	L 17–18	V41	L 17–30	V73	L 01–31	V105	L 24–37
V10	L 19–25	V42	L 18–27	V74	L 31–32	V106	L 18–40
V11	L 22–24	V43	L 18–28	V75	L 32–33	V107	L 13–24
V12	L 20–22	V44	L 18–29	V76	L 13–33	V108	L 09–24
V13	L 21–23	V45	L 18–30	V77	L 02–34	V109	L 05–24
V14	L 01–22	V46	L 05–25	V78	L 16–34	V110	L 01–24
V15	L 05–22	V47	L 09–25	V79	L 03–35	V111	L 01–13
V16	L 09–22	V48	L 13–25	V80	L 15–35	V112	L 36–37
V17	L 13–22	V49	L 01–19	V81	A 01&05-A09&13	V113	L 02–16
V18	L 22–31	V50	L 05–19	V82	A03&07-A11&15	V114	L 03–15
V19	L 05–31	V51	L 09–19	V83	A05&01-A24&20	V115	L 03–24
V20	L 22–33	V52	L 01–02	V84	A09&13-A20&24	V116	L 07–24
V21	L 09–33	V53	L 02–03	V85	A03&01-A01&13	V117	L 11–24
V22	L 22–32	V54	L 03–04	V86	A07&05-A01&13	V118	L 15–24
V23	L 32–34	V55	L 01–04	V87	A11&09-A01&13	V119	Area 01
V24	L 34–35	V56	L 05–06	V88	A15&13-A13&01	V120	Area 02
V25	L 26–35	V57	L 06–07	V89	A01–22-05	V121	Area 03
V26	L 01–05	V58	L 07–08	V90	A05–22-09	V122	Area 04
V27	L 05–09	V59	L 05–08	V91	A09–22-13	V123	Area 05
V28	L 09–13	V60	L 09–10	V92	AO2–25-19	V124	Area 06
V29	L 13–19	V61	L 10–11	V93	A16–19-25	V125	Area 07
V30	L 19–20	V62	L 11–12	V94	A01–24-05	V126	Area 08
V31	L 24–25	V63	L 09–12	V95	A05–24-09	V127	Area 09
V32	L 01–25	V64	L 13–14	V96	A09–24-13	V128	Area 10

a cluster dendrogram predicted the number of individuals (Alibhai et al., 2017; Jewell et al., 2016). Trails predicted to be from the same individual were color-coded and clustered together on the dendrogram (See Fig. 5 section 3.6 below, and Supplementary Figs. 3–6).

3. Results

3.1. Data collected from captive Amur tiger

Data were collected from 44 captive Amur tigers of known identity, age and sex, to form the basis of the footprint identification algorithm for individual identification. The tigers ranged from 3 to 13 years of age. Four classes of age were created for the subsequent investigation of age-related footprint metrics; Class A (<5 years of age), Class B (5–8 years of age), Class C (8–11 years of age) and Class D (11 to 13 years of age). Between 7 and 23 high quality left hind footprints were collected from each individual tiger. Where >10 left hind footprints were collected, they were divided arbitrarily into sub-trails to provide a larger number of sub-trails for analysis. Supplementary Table 1 summarizes the data collected from captive Amur tiger.

3.2. Data collected from free-ranging Amur tiger

Trails were collected from free-ranging Amur tiger, of unknown identity, at the study sites. Table 2 reports the trail ID collected for each trail. As described above (Section 3.1) sub-trails were formed where >10 footprints existed in any one trail. For example, the table indicates that using the 25 left hind footprints from trail MW09, we were able to derive four sub-trails. Section 3.5 below explains how the sex classification for images and the resulting designations for each trail were made.

3.3. Data validation to determine the optimal size for algorithm training and test sets

Data validation was performed on the captive Amur tiger dataset to determine the optimal number of footprint trails required for the algorithm training set and test sets that could provide an accurate population estimate. Fig. 4 shows the result of a holdback trial partitioning test on training sets for 44 captive Amur tigers. Using the algorithm generated in FIT, the analysis was iterated 10 times for each combination of test/training size, with randomly selected trails, to examine how the predicted outcome compared with the known test set size. The figure shows, for example, that then the test set size (y axis) comprises trails from 4 tigers, and the test/training set size comprises trails from 04/40 tigers, the predicted test set sizes are very similar across a range of partitioning trials. However, when the test set size is 36 tigers, and the test/training ratio 36/08 tigers, there is a wide range of predicted test set sizes and the mean of the predicted test set size diverges from the actual test set size.

Optimal classification accuracy was obtained when the test set size was smallest relative to the training set. However, even when the test to training set ratio was 32:12, the predicted value was close to the expected value, demonstrating the robustness of the model.

3.4. Algorithm training using data from captive Amur tigers

A classification dendrogram was generated using the FIT pairwise comparison model for 44 trails from captive Amur tigers (Supplementary Fig. 3). The process was iterated multiple times by altering elements within the model to generate the fewest misclassifications (Li et al., 2018). The final classification model correctly predicted 44 tigers giving 100% accuracy. This algorithm was then used to classify the free-

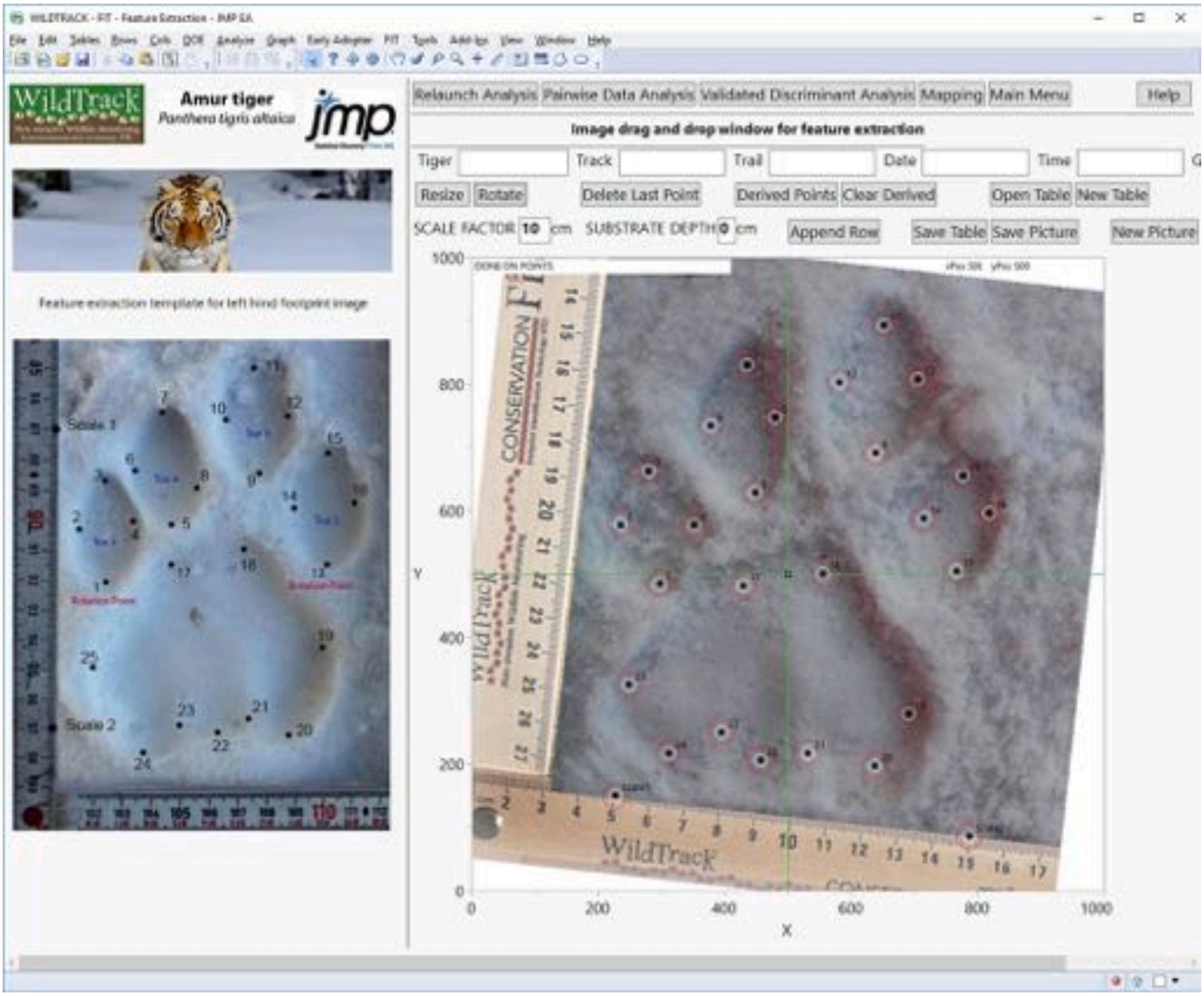

Fig. 3. The Footprint Identification Technique (FIT) feature extraction window in JMP software for the extraction of variables from the footprint. The left side of the window holds a template for the position of landmark points and the scale markers. The right side of the window, the active section, allows the drag and drop of sequential field images for analysis. Twenty-five landmark points and fifteen derived points are positioned on each footprint.

Table 2
Footprint trails collected from free-ranging Amur tigers in 2012 & 2015/16 at three different locations, showing the trail label, number of usable left hind footprints, number of sub-trails, sex predicted for individual images, sex predicted per trail, image collection date and location site of trail.

Trail ID	No. usable left hind images	No. sub-trails	Sex id of images (M/F)	Sex designation per trail	Image collection date	Location site of trail
FW1	13	02	2/11	F	2012	A
FW2	12	02	3/9	F	2012	A
FW3	14	02	2/12	F	2012	A
FW4	13	02	0/13	F	2012	A
MW5	13	02	13/0	M	2012	A
MW6	04	01	4/0	M	2012	A
MW7	06	01	5/1	M	2012	A
FW8	04	01	1/3	F	2012	A
MW9	26	04	25/1	M	2015/16	A
MW10	12	02	11/1	M	2015/16	B
FW11	02	01	0/2	F	2015/16	B
FW12	02	01	0/2	F	2015/16	C

ranging trails (Alibhai et al., 2017).

3.5. The individual classification of free-ranging Amur tigers

Using the algorithm derived from captive Amur tiger footprints, a trail classification dendrogram was generated for free-ranging Amur tigers of unknown identity, using the 13 trails collected in 2012 at location site A (Supplementary Fig. 4). The FIT predicted a total of 7 tigers, 4 females and 3 males, with all sub-trails correctly classified. Footprints for the trails were independently subjected to sex discrimination analysis (Gu et al., 2014).

Table 2 (see also 3.2 above) shows the distribution of footprints classified as male or female for each trail. The trails and sub-trails for free-ranging tigers were classified by sex as F (female) or M (male) using the method described by Gu et al., 2014. A total of 212 footprint images were collected from 12 trails and subjected to sex discrimination analysis. Based on classification within trails, of the 121 images 11 were not consistent with the majority of images in each trail, giving an accuracy of 90.1%. An analysis for females gave 8 inconsistently assigned images out of 60 (accuracy of 87%). For males, 3 images of 61 were inconsistently assigned giving an accuracy of 95.1%.

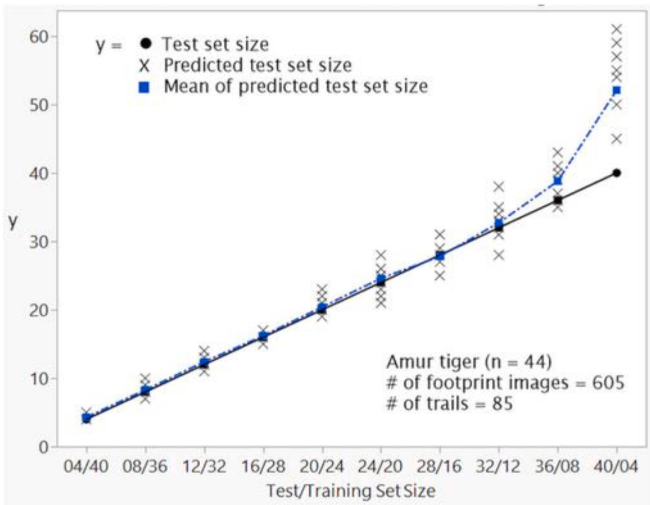

Fig. 4. Holdback partitioning trials using test and training sets. The test set size was plotted against itself (black circle), against the predicted value for the test size (black X) and against the mean predicted value for each test size (blue square).

A trail classification dendrogram for individual identity was generated from 4 trails collected at sites A, B and C, from free-ranging Amur tigers in 2016. The FIT predicted 4 tigers with all sub-trails classifying correctly (Supplementary Fig. 5). A trail classification dendrogram was generated from 11 trails collected from free-ranging individuals in 2012 and 2015/2016 and predicted 11 individuals. All self-trails were clustered correctly together (Supplementary Fig. 6).

3.6. The classification prediction of Amur tiger using images collected from both captive and free-ranging individuals

All footprints from both captive and free-ranging Amur tiger footprint were then analyzed together, with a resulting 6 trail misclassifications. The analysis predicted of 54 individuals against the expected 55 individuals (44 known captive, and 11 were predicted from free-ranging prints). In this analysis of all individuals, the classification accuracy of self-trails for free-ranging individuals remained unchanged and was similar to the results of the analysis performed for captive and free-ranging animals separately.

3.7. The distribution of total footprint area by sex, for captive and free-ranging Amur tigers

Using linear discriminant analysis, we identified Area 1, the total footprint area, to be the most significant measurement (assessed by the highest F-ratio) differentiating males from females. Although there was natural variation in Area 1 within each sex and age class category, the distribution pattern for the males and females exhibited a marked difference. The Area 1 measurement for adult females (> 3 years) across all age classes did not vary markedly. However, for males, age classes A and B exhibited the highest means, with a clear decline in Area 1 size in the older age-classes. At 12 years of age, the male footprint size (Area 1) was significantly smaller than that for individuals in age classes A & B (Anova $F_{1,120} = 30.49$, $p < 0.0001$) (Fig. 6).

A similar difference between male and female free-ranging Amur tigers emerged (Fig. 6). Trails FW2 & FW3 which were classified by FIT as belonging to the same female appear to have very similar distributions and means.

4. Discussion

4.1 The FIT described in this paper offers some advances over previous analytical footprint identification techniques in the following ways: it has developed a standardized protocol for footprint collection thus reducing observer bias in processing, it extracts more metrics from each footprint thus providing a greater opportunity to select truly discriminating metrics and develop a robust training set, it analyses more footprints per animal in the training datasets to adjust for individual variation, it integrates algorithm validation, and it offers these advantages within a fully integrated software interface that reduces the risk of subjective interpretation (Alibhai et al., 2017).

4.1. Individual identification model determination and predictions

Our best-fit model correctly predicted the number of captive tigers. Without information on the identity of the free-ranging tigers from whom we collected trails, we were unable verify our prediction for their numbers. However, the derivation of 128 variables from each footprint, together with a statistically robust model and data validation steps suggested that the classification model had correctly identified the free-ranging Amur tiger trails. In addition, the predictions given by analyses done separately for 2012, 2015–16 and both together were consistent. Furthermore, there was agreement between the classification of trails by sex first, and then by individual identity. Nevertheless, further validation of this technique for application to free-ranging tigers should be undertaken using a population of known individuals and, ideally, testing alongside other techniques that have already been validated in the same conditions.

Further algorithm validation was undertaken using holdback trials, to establish the minimum number of trails required for testing. Although the predicted mean for each test:training set size was close to the actual test size up to the 32:12 combination, after a ratio of 20:24 the amount of variation in the sequential trials increased, potentially resulting in reduced algorithm accuracy.

4.2. Sex and age determination

We used the sex identification method described by Gu et al. (2014) to investigate the relationship between the area of the foot (Area 1) for the two sexes across a range of age-classes, where the FIT algorithm for sex determination gave 98% accuracy for individual footprints. The larger size of Area 1 in males is consistent with the sexual dimorphism in Amur tigers - mature males are significantly larger than mature females (Sunquist and Sunquist, 2002). Investigating this variable by sex and age-class revealed a decline in Area 1 size in older males. It is possible that a decrease in footprint size might signify a contraction of ligaments or increase in foot musculature with age, but one might reasonably expect this to apply to females also and the observation remains to be explained.

Over decades of monitoring Amur tigers in both Russia and China, field workers have identified Amur tigers by sex or individual using simple measurements of front pad width, using assumptions about individual range (Hayward et al., 2002). A limitation in this system has been the difficulty in discriminating between adult females and subadult males. The interaction between age and sex for footprint identification is thus of practical importance in understanding Amur tiger populations. As an example, the Amur Tiger Monitoring Network (Zhang et al., 2012) seeks to understand the ecology of resident female Amur tigers as an indicator of local population recovery (Goodrich et al., 2010). Our study demonstrated that FIT was able to identify individuals (including sub-adult males and adult females) with >90% confidence (Fig. 5) and that despite overlapping ranges of measurements for foot areas, the means for subadult males and adult females were sufficiently different to be discriminated using trails of footprints.

Sex identification was also used as a filter to help establish the identities of Amur tigers from free-ranging trails. 5 of the 12 trails exhibited consistent sex classification for all footprints, with the remainder exhibiting a clear majority for either male or female. This also

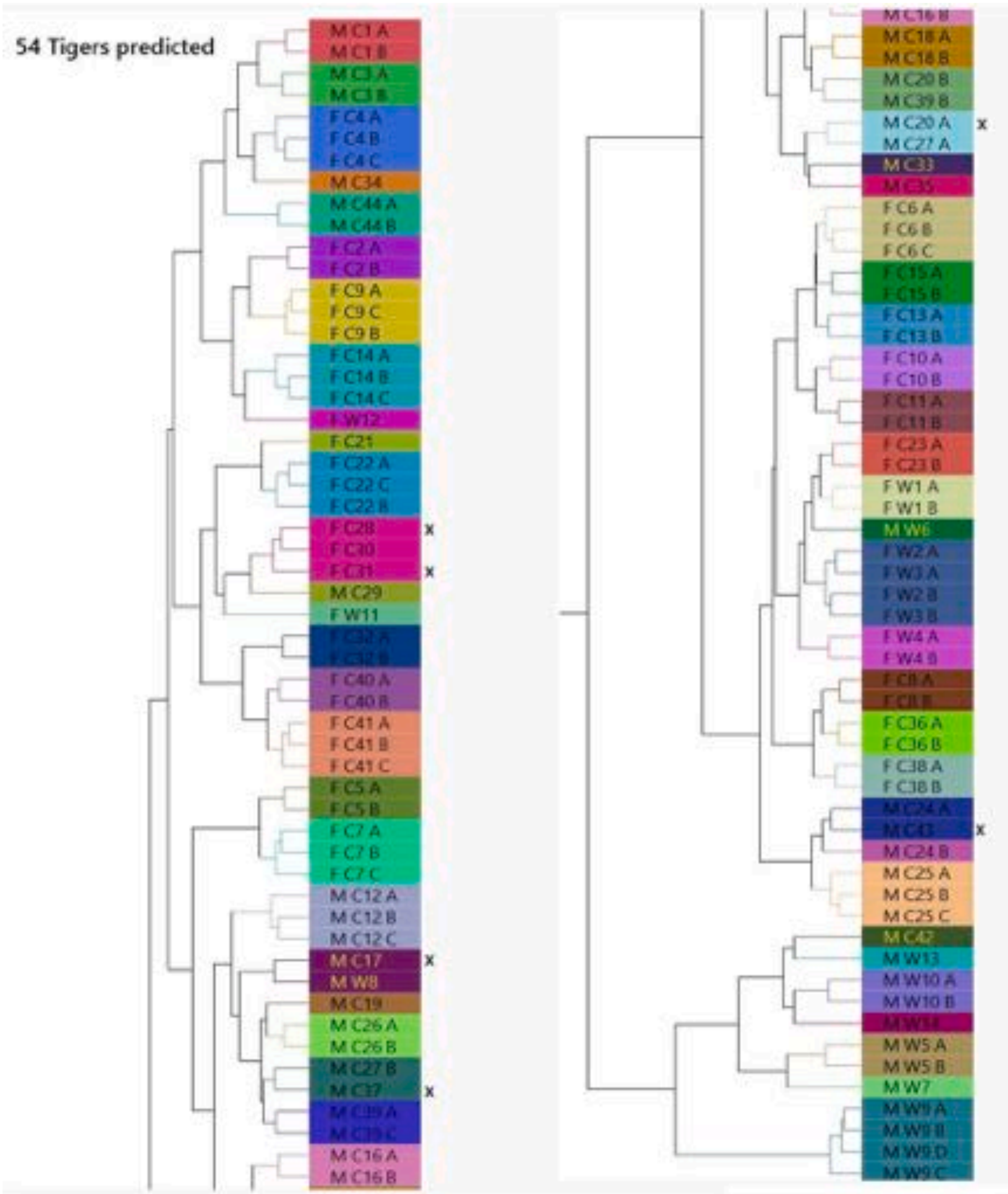

Fig. 5. The trail classification dendrogram for captive and free-ranging (2012 and 2015/6) Amur tigers showing the predicted total number of individuals (54), and the classification of self and non-self trails. X indicates misclassified trails (7 of 106).

provided consistency with the individual identification of trails.

4.3. The use of footprints for censusing and monitoring big cats

The use of animal footprints ('pugmarks') for tracking and monitoring has been described as the origin of science (Liebenberg, 2013) and was undoubtedly instrumental in human evolution. In 1966 Indian forester S.R. Choudhury (Choudhury, 1970, 1972) developed a basic 'pugmark' census for monitoring the Bengal tiger throughout India. Thousands of foresters, members of local communities and many with tracking skills, traced or collected plaster casts of footprints found. They arrived at local, regional and then national population estimates through simple visual comparisons, tracings, and/or basic measurements of the footprints collected, in combination with local knowledge that enabled assumptions about local tiger ranges. Singh (1999) remarked that this technique yielded accurate results in a cost-effective and practical manner.

Karanth et al. (2003a) argued that this survey method was statistically unreliable because of three fundamental failures: a failure to identify all possible footprints, a failure to correctly identify the

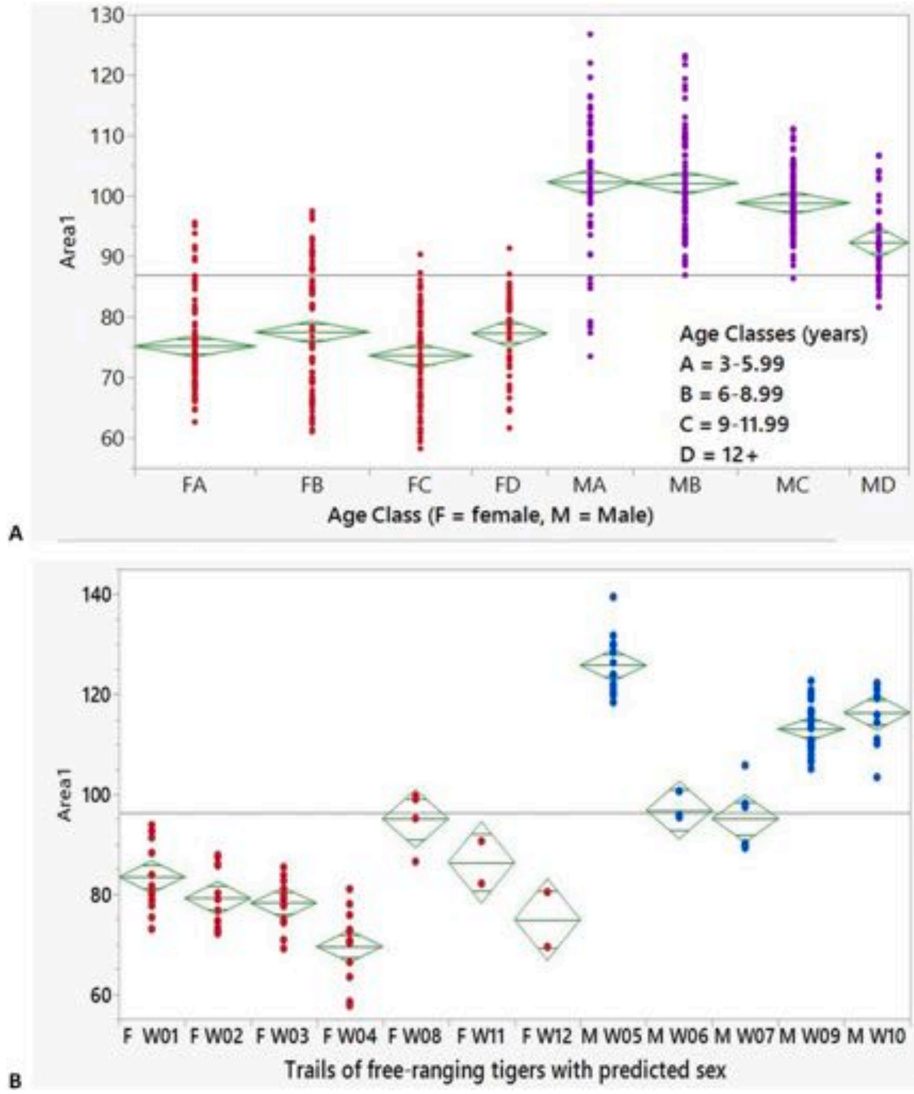

Fig. 6. a. The sex and age-class distribution for captive Amur tiger trails by Area 1 (total foot area). Fig. 6b The sex and age class distribution of Area 1 (total foot area) for free-ranging Amur tigers.

appropriate footprint, and a failure to recognize individual tigers. An argument was made for a national transition to camera-trapping techniques. and the all-India pugmark census was replaced by sampling smaller areas using camera-traps. Tiger population estimates decreased, and it was widely reported in the press that the pugmark technique had resulted in over-counting (Karanth, 2003).

Whilst the basic approach of the pugmark technique led to inaccuracies of population estimates, we have demonstrated in this study that a robust and statistically valid approach such as FIT, if included in a methodological framework that can satisfy sampling-based survey methodology requirements (Gopalaswamy et al., 2019), has the potential to be a useful tool to provide optimal census and monitoring capability through tiger ranges. When FIT is used by data collection teams that have even rudimentary tracking skills, it can overcome the reservations put forward about the use of footprints for conservation monitoring (Karanth et al., 2003). For example, field operatives with very basic training or accompanied by trackers can identify left and right hind footprints and collect images according to the FIT protocol (an app is being developed to collect the necessary images with smartphones). The FIT integrated software provides local ecologists with the ability to identify individuals, sex, and age-class. If trackers are not available to cover all the required areas, footprints could be used as 'marks' in mark-recapture protocols in selected areas, in much the same way as camera trap images are (Jewell et al., 2016). Footprint identification is also independent of coat-pattern, as has been described for the mountain lion (Alibhai et al., 2017) and work is underway to monitor this species in snow substrates in the Americas. Our experience has shown that heterogeneity of substrate can be accommodated if representative data from the different substrates are included in the model.

FIT can also be deployed at different levels of granularity (Jewell et al., 2020). Where a census is required, the collection and processing of footprints can provide a prediction of the total number of animals represented by those footprints. Where information on the movement or behaviour of individual animals is required, footprints are first mapped to a known individual and thereafter it can be monitored using footprint identification. For example, in reintroduction or translocation settings where individuals can be characterized prior to release, their subsequent movements can be ascertained by footprints. These ecological data can provide insights into the range changes, activity levels, interaction with other individuals and many other crucial aspects of success of reintroduction in the long term.

Footprint identification techniques, like other monitoring methods, have constraints. Where footprints do not form, or are visible for only a short time, data collection may be challenging or even impossible. Furthermore, FIT requires footprints that have clear outlines of toes and heel pads which may not always be possible in unsuitable substrates. In situations where field data collectors have no experience locating footprints, or there are no local trackers available, it may also be difficult to collect enough data. The existence of footprints is also dependent on the vagaries of the weather, and so planning a short window of fieldwork with no flexibility can present further challenges. In areas where population densities are extremely low (as reported in this study), finding enough signs (in this case footprints) for a full survey may be challenging, and require more effort, but this applies to most if not all techniques for monitoring populations that exist at low density. No longitudinal studies have yet been undertaken to assess the variability of footprints over time and this is an area worthy of investigation. Our preliminary field observations suggest that frequent monitoring might allow changes in track size and shape over time to be incorporated in the database and resulting identification algorithm.

There are few studies comparing the efficacy of many different non-invasive approaches carried out simultaneously in the same area. However, one comparison of six methods for estimating Amur tiger abundance in Russia's Sikhote-Alin Biosphere region was undertaken by Riley et al., 2017. Camera-trapping, DNA from hair and feces, scent-tracking dogs, morphometric track identification and track index survey methods were assessed. However, a paucity of data resulted in effective evaluation of only three approaches: camera-traps, DNA collection and track index surveys. DNA collection and camera traps were considered statistically acceptable but performed poorly on indicators of cost and logistics. In contrast, track index surveys proved the most efficient logistically and financially, and were able to be applied on landscape scales, but failed to satisfy the statistical criteria set by the team. The track ID method, based on an objective approach described by Sharma et al., 2005, failed because survey teams were unable to obtain enough data at the field site during the study period.

Camera-trap techniques may also present constraints. Where unique coat patterns or other morphological features are absent, camera traps are impractical for identifying individuals. Even when morphological features are present, identification may be challenging. Johansson et al. (2020) reported that identifying individuals with unique coat patterns from camera-trap photos may not be as reliable as previously believed, citing a lack of empirical evidence to verify the assumption that individuals (even those with unique coat patterns) are accurately identified in studies that rarely report how identification was performed. Johansson et al. (2020) also noted that there is no baseline measure of classification error in these species because studies have not been undertaken to measure classification accuracy in a population of individuals with known identity. Thus, it is currently unknown how much observational uncertainty is associated with classifying images of species with individually-unique markings, and how this subsequently influences confidence in abundance estimates. However, as machine learning and computer vision techniques advance it is likely that they will offer increasingly reliable alternatives to human assessment for camera-trap images (Hermona and Sharmab, 2021) and possibly also footprint identification. Another potential camera-trap consideration is that tigers have been noted to avoid them, and potentially any such intrusion may limit the ability of conclusions to be drawn from animal behaviour obtained by camera-trapping (Meek et al., 2016; Wegge et al., 2004). Caravaggi et al. (2020) review camera-trap literature and identify three key challenges: disturbance caused by cameras, variation in animal-detection parameters across camera models and biased detection across individuals and age, sex and behavioural classes. Finally, and perhaps most critically for sustainable conservation initiatives, camera-traps rarely engage the traditional ecological knowledge and skills of local communities in the way that tracking techniques can. They are extremely sensitive to changes in layout design and set-up, requiring expertise that is not often found in local communities. Jhala et al. (2021) discuss at length the importance of engaging local communities in the cause of tiger conservation.

4.4. Field application potential for Northeast China

We have described the application of the FIT to identify and monitor individual Amur tigers in the wild. Amur tiger populations are very sparsely distributed over a huge and generally resource-poor area, particularly in Northeast China. This delivers specific challenges for monitoring. While SECR offers freedom from the need to prove a 'closed' population, it requires density estimations to be based on an explicit spatial component of each individual's detection history and a defined state-space over which density is estimated. Because of these additional requirements, SECR models can be more data hungry than the traditional closed capture-recapture models. Augmenting data collection through citizen science could improve the reliability of such estimates (Green et al., 2020). Footprints have traditionally been used as part of a monitoring strategy in these areas (Hayward et al., 2002) and FIT offers the opportunity to augment data from camera-traps or other non-invasive techniques, and when including local community trackers and hunters, it strengthens the reliability of detection and identification of individuals. As global tourism recovers from the impact of the Covid-19 pandemic, the upcoming development of a user-friendly FIT data collection app to record footprints will facilitate the engagement of this growing resource. One often overlooked issue in the discussion of monitoring approaches was raised by Riley et al. (2017) who noted that while occupancy patterns (derived from sampling) may be sufficient for population monitoring, nearly all government agencies are pressured to report absolute abundance. The cost and logistics of providing these figures must be taken into account in resource-poor areas. In addition, relying predominantly or exclusively on a method that depends on external experts (DNA analysis, camera-trap analysis) ignores the advantages conferred when conservation infrastructure is self-reliant. 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.

4.5. Comparative material costs for implementation of FIT

The equipment required for the implementation of FIT is minimal. A basic digital camera (e,g. a Sony CyberShot) or smartphone can capture data at a minimum recommended 1600×1200 pixels. A metric scale is required. Images can be stored on an external or cloud-based drive. A standard home-office laptop computer can run the required analyses. In areas where human resources are already deployed for monitoring at-risk species (eg anti-poaching or community-outreach), data collection can be integrated at very little extra cost. In areas where this is not the case, salaries for data collectors are required for fieldwork, but this comes with the benefits of community capacity-building. The costs of implementing camera-trap or eDNA survey for low density populations may be considerably higher but will vary greatly depending on the area to be surveyed and local costs. Jewell et al. (2020) offered a qualitative comparison of commonly used rhino monitoring techniques, in terms of their speed, accuracy, estimated relative cost and suitability for local conditions, that might provide a template for a future big cat monitoring study.

4.6. Final considerations

There are many considerations to be made when selecting a monitoring method for big cats, and a full review is beyond the scope of this paper. It is clear from the literature, however, that all available techniques for censusing and monitoring present both challenges and opportunities. We recommend the deployment of a toolbox of non-invasive and cost-effective techniques best suited to local resource availability, environmental constraints and the reporting requirement. For small areas, monitoring individuals with distinguishable coat-patterns, where there is a relatively high population density and sufficient funding, camera-traps may be preferable. If those areas present opportunities for footprint collection, FIT could be combined with the traps for a broader-spectrum survey. For regional and landscape-scale areas where resources are scarcer, and more cryptic and elusive animals live at low densities, objective footprint identification and scent dogs, with selective use of eDNA or camera-traps combined into a statistically acceptable but accessible framework may be preferable (Lyet et al., 2021). In many situations, a combination of camera-traps with footprint identification technologies, both non-invasive and thus animal-friendly, could provide an ideal basis for a broad-spectrum community-based survey and we intend to identify research partners to test this combination in the field. The rapid emergence of computer vision techniques promises to hugely augment both the speed and breadth of data processing for both footprint and camera-trap techniques. Beyond selection of the ideal monitoring tool(s), it is worth reflecting that where population declines are linked with human conflict, local community engagement in the conservation effort can be transformative (Dheer et al., 2021).

Declaration of Competing Interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data availability

We have shared the link to our data at the 'attach file' step

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2022.101947.

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