Using Patterns in Track-Plate Footprints to Identify Individual Fishers

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ABSTRACT If individuals can be identified from patterns in their footprints, noninvasive survey methods can be used to estimate abundance. Track plates capture fine detail in the footprints of fishers (*Martes pennanti*), recording rows of dots corresponding to tiny papillae on the animal's metacarpal pad. We show that the pattern of these dots can be used to identify individual fishers, similar to human fingerprints. A probabilistic model of uniqueness based on variation in spacing between 1,400 pairs of dots that we measured in prints of 14 different fisher feet suggests the probability of encountering a similar pattern in the print of a different foot by chance alone is <0.35ⁿ, where n = the number of dot pairs examined. This predicts a 0.00003 probability that a match made using 10 pairs of dots is false. Dot spacing from footprints made by the same foot was remarkably consistent ($\sigma = 0.02$ mm, n = 24 dot pairs). Combined, these results suggest dot patterns in fisher footprints were unique to individuals and were consistently reproduced on track plates. Empirical tests of matching accuracy were best with good-quality prints, highlighting the need for experience judging when prints are usable. We applied print matching to fisher detections collected on track plates deployed at 500-m intervals along 10 3.5-km transects in the Adirondack region of New York, USA. Of 62 fisher detections, 85% had ≥ 1 footprint of suitable quality to compare with other high-quality prints. We found that most detections from a transect were from the same individual fisher suggesting nonindependence of detections. Thus, data from traditional track-plate deployments over small time periods cannot be used as a measure of abundance, but new study designs using print matching could obtain robust noninvasive, mark-recapture density estimates. (JOURNAL OF WILDLIFE MANAGEMENT 71(3):955–963; 2007)

DOI: 10.2193/2006-408

KEY WORDS census, fingerprint, fisher, footprint, identification, Martes pennanti, track plate.

Establishing and monitoring abundance of rare species remains a challenge, particularly for forest mammals. Abundance data can be collected through live-trapping but this is invasive and can be logistically difficult at scales relevant for wide-ranging species. As a result, there has been increased attention paid to methods of obtaining abundance information over large areas that are noninvasive and require less manual labor (Zielinski and Kucera 1995, Harrison et al. 2002, Gompper et al. 2006).

Accurate methods to estimate abundance require unambiguous recognition of individuals (Otis et al. 1978). Identifying individuals through genetic fingerprinting of hair or feces is increasingly common but can be expensive, laborious, and error prone (Woods et al. 1999, Creel et al. 2003). Camera traps are increasingly favored for carnivore surveys but, when applied to density estimation, generally are limited in usefulness to species with individually unique pelage patterns (Karanth 1995, Karanth and Nichols 1998, Trolle and Kéry 2003) or populations that have been otherwise captured and tagged with large unique markers (e.g., ear tags; Fuller et al. 2001). Foot prints from natural substrates and track-boxes have long been used to identify species presence. Some efforts have been made to identify individuals of certain large species from gross footprint morphology (Panwar 1979, Riordan 1998, Jewell et al. 2001, Sharma et al. 2005), but these methods have not been widely applied and their validity has been questioned (Hamm et al. 2003, Karanth et al. 2003).

Although observational studies routinely use unique animal pelage patterns or facial markings to identify individuals (e.g., Goddard 1966, van Lawick-Goodall 1968, Peterson 1972, Scott 1978) most do not address the possibility of pattern duplication across individuals and variability is assumed to result in combinations that are unique or at least practically unique. A few studies have used rudimentary information-theory techniques (Shannon 1948) to estimate the likelihood of a duplicate occurring given the overall frequency of character occurrence (Pennycuick and Rudnai 1970, Miththapala et al. 1989). The most rigorous analyses of individual marking uniqueness have come from the study of human fingerprints (e.g., Roddy and Stosz 1997, Pakanti et al. 2002). These include creation of statistical pattern-models to estimate the probability of false duplication, and empirical comparisons of a large number of prints using a defined matching technique.

The purpose of our study is to show that individual fishers (*Martes pennanti*) can be recognized from footprints made at enclosed track-plates and to apply this method to field data obtained from free-ranging fishers.

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STUDY AREA

We conducted field work in northern New York, USA, in and around Adirondack State Park (approx. 25,000 km²), the largest park in the contiguous United States (Jenkins 2004). Our 54 field sites were throughout the park and surrounding region in a variety of forested and anthropogenic habitats.

METHODS

Comparing Fisher Footprints—General Considerations

We used 3 levels of detail for individual identification (Fig. 1). At the coarse level of detail we used overall size and shape of the footprint outline. Although variation at this level is insufficient to conclude 2 footprints are the same, a large difference between the size of 2 prints can confirm they are different (Foresman and Pearson 1998, Hamm et al. 2003). At the intermediate level of detail we used patterns formed by the curving rows of dots. We found that pattern variation between individuals was not great at this level, and their perception varied between observers. Therefore, their definitive usefulness was limited when comparing footprints. For fine-scale detail, we used the small dots created by the papillae (i.e., bumps) on the bottom of the foot. Spacing of these dots was highly variable between individuals. These details were the primary focus of our comparisons.

Although fine-scale detail formed the basis for individual identification, we evaluated footprints at higher levels to determine which foot made the print. For example, footprints made by left forefeet should only be compared to other prints made by left forefeet. We identified which foot a print came from using 3 criteria: 1) footprints from left feet are usually found on the left side of the tracking surface, although this is not always the case; 2) the impression made by the first (most medial, often not visible) toe introduces an unambiguous asymmetry, and toes 2-5 of the forefeet angle toward the medial side; and 3) the metacarpal pad outline typically displays asymmetry for front feet (Fig. 2). Rear feet appear less often and we did not use them to identify individuals, but we identified rear footprints by toes 2-5 pointing straight ahead and a symmetrical metatarsal pad impression. Intermediate-level details are also useful to differentiate feet because row patterns are more or less bilaterally symmetric, with left and right metacarpal pads being rough mirror images of each other (Fig. 2). This is most evident in the center of curvature for the arcs formed by each row of dots located in the upper right of the metacarpal pad for right feet and in the upper left of left feet.

Digitizing and Comparing Footprints

We used a desktop image scanner (Hewlett Packard 4570c; Hewlett Packard, Palo Alto, CA) to create digital images of footprints at a resolution of 2,400 dots per inch. Our calibration tests for all regions of the scanner's working surface found horizontal and vertical measurement resolution of 0.01 mm. We also used photographs of footprints that we took with a high-resolution (\geq 4 megapixel) digital



Figure 1. Right front footprints of the metacarpal pads of 3 different fishers showing the patterns of dots used to distinguish individuals. Dots in the images are impressions of papillae that cover the pad. We made these prints with fisher specimens at the New York State Museum, New York, USA.

camera. Gray-scale images (256 levels) were adequate and resulted in smaller file sizes than full-color images.

We measured and visually compared footprint images by counting pixels using image-processing software. Many commercial packages were suitable but we used IMAGEJ (http://rsb.info.nih.gov/ij/), free software written in the Java programming language. It runs under many operating systems, has full image processing functionality, and the source code is freely available. The basic technique for comparing 2 footprints consisted of aligning and magnifying images while repeatedly switching between them, looking for matching dot patterns (Fig. 3). We typically started by focusing on a particularly clear and unique dot in one print, and tried to find its match in the second print. We confirmed 2 prints to be the same after matching a number of dot pairs, or we rejected 2 prints by failing to match them after sufficient search. We have provided an online tutorial at http://www.nysm.nysed.gov/research/ biology/fisher/index.html.

This technique assumes that general rotational alignment of the 2 images is similar. A small amount of rotational



Figure 2. Characteristics of prints made by each foot of a fisher. We use the shape of the metacarpal pad, patterning of dots in the metacarpal pad, and angle of the toes to identify which foot made a given print.

misalignment, however, actually helped distinguish matching areas, as rotating movement was easier to recognize than simple linear translation. We found $5-10^{\circ}$ of misalignment gave the appearance of rotating movement when images were rapidly switched back and forth. Lack of this effect indicated either nonmatching images or poor alignment (see animated example at http://www.nysm.nysed.gov/research/ biology/fisher/matching_method_introduction.html). When we positioned 2 images such that corresponding dots were directly aligned, these became the center of rotation as we switched images. We considered the prints a match when this center of rotation could be repeated with several



Figure 3. Fine-scale views of 4 different left front prints made by the same free-ranging fisher in the Adirondacks of New York, USA. We identify 7 corresponding dots in each image, although many more can also be seen in this comparison.

different dot pairs across the print. Although spacing of any pair of neighboring dots varied little between different prints, the relative position of dots that are not close neighbors will change noticeably because of pliability of the living foot. Thus, only neighboring dots should be examined for matches. Prints may need to be slightly realigned when examining different regions of the prints.

Footprint Quality and Distortion

Poor print quality results in greater difficulty identifying corresponding dot patterns between footprints, thus increasing potential for error. We categorized footprints according to 3 levels of quality. Good-quality footprints had no major distortion and contained distinct dots in all or most of the main portion of the metacarpal pad. Relatively few dots were smudged or obscured. Fair-quality footprints exhibited characteristics of a good print over half of the pad or less. Assuming the portion was large enough for the desired confidence level, one could readily match goodquality footprints or to other fair-quality prints if each shared the same clear area. Poor-quality footprints were not matchable because they lacked the minimum number of distinct dots to be confidently assessed or because they were so incomplete that orientation of the candidate footprint vis-à-vis the reference print was not possible.

Ensuring Sufficient Matching Effort

Positive indication that 2 footprints match was clear; confirming a nonmatch was more difficult, especially with poor-quality prints. If 2 footprints did not match, we considered 3 possibilities: different source individuals, examiner error, or poor-quality prints. Experience with prints of known origin helps make this judgment, as does reexamining coarse- and intermediate-level details. Finally, we systematically shifted one image relative to the other by small amounts, in both horizontal and vertical directions, until all possible reasonable combinations of alignment had been checked to eliminate the possibility that prints were the same. With practice we found that this process usually took <5 minutes.

Footprint Uniqueness and Repeatability

Even though fine-scale patterns on foot pads from different fishers were highly variable between individuals, footprints gathered in the field sometimes lacked the clarity, detail, and completeness necessary to reveal variation. Therefore, it was important to develop some measure of how much pattern information would permit the examiner to conclude 2 footprints are or are not the same. Because even simple information theory was difficult to apply to such complex patterns (Pakanti et al. 2002), we used theory developed for the study of human fingerprints. Specifically, we used the sub-discipline of fingerprint forensics known as poroscopy or identification based upon patterns of pores in the skin (Ashbaugh 1982, Roddy and Stosz 1997).

We analyzed rarity of foot-pad patterns using front footprints made using museum fisher specimens by applying ink to foot pads and pressing the pad onto paper. Because museum specimens lacked the pliability of live feet, patterns from multiple prints made by the same foot exhibited virtually no variation. This made them useful for examining variation between individuals without concern for differences between multiple prints made by the same foot. We examined 14 feet from 10 individuals (6 M, 4 F). The sample included left (n = 10) and right feet (n = 4). We measured the distance between centroids of adjacent dots within the same row, performing 100 measurements on each foot (total = 1,400). From these we determined the probability of occurrence for the most common spacing $(P_{\rm R0})$ and used it to develop a probabilistic model of dot patterns in a fisher footprint. We used this to predict the odds that 2 print segments made by different animals' feet will match by chance alone, depending on the number of dot-pairs matched. Thus, in addition to demonstrating that foot-pad patterns were sufficiently unique, the model also estimated rarity for smaller portions (subset of the dot-pairs) of the pattern. This was important given that footprints collected in the field often provided clear patterns for only part of the print.

We used a model that approximated patterns in fisher metacarpal pads as a series of parallel rows of dots with variable distance between neighboring dots. Assuming that spacing between any pair of dots was independent of the spacing for nearby pairs, the most common arrangement will be when all spacings are equal to the median value (P_{R0}) . To investigate whether spacing between dot pairs was independent of spacing for nearby pairs (i.e., autocorrelation) we measured the spacing of 100 neighboring dot triplets resulting in sets of 2 spacing measurements, and we evaluated the correlation coefficient between paired distances. To measure the magnitude of this effect, we identified 196 cases of the most common spacing (0.22-0.28 mm) and measured 306 adjacent dot distances. We determined the percentage of adjacent spaces that also fell within the range 0.22-0.28 mm and compared that to the percentage predicted by the overall distribution of spacings.

Because deviation from the pattern where all dot spacings equal the median value represents a less likely combination, the probability of occurrence of the most common condition is an upper limit and conservatively estimates pattern rarity. When applied to an arbitrary number of dots, the maximum probability of occurrence for that portion of a footprint equals the product of the probabilities of occurrence for each encountered spacing. Thus, the maximum (i.e., most conservative) probability of occurrence for a particular pattern of dots within a row, P_{n_i} is:

$$P_n \le P_{R0}^{\quad n} \tag{1}$$

where n is number of spaces between neighboring dots of the same row. Equation 1 could be restructured to solve for n, the number of corresponding dots one must match between 2 footprints to know with some degree of certainty that the same foot made those 2 prints. The possibility that 2 footprints made by different animals' feet will match by chance alone can be set arbitrarily small by increasing the number of dot pairs matched.

As an empirical evaluation of accuracy, we constructed a test consisting of 8 triads of prints (4 good quality, 4 fair quality) collected in the field, including 2 known matches and one known not to match. Using the methodology to select the matching pair, 9 biologists took the test; 4 had previous practice examining prints. To determine variation in pattern over time we compared centroid-to-centroid distance for dot pairs across different prints from the same foot of the same animal. We used measurements from 3 feet of 2 individuals (2 front feet from an unknown sex individual, 1 left foot of a M fisher). We examined 7 footprints, 8 footprints, and 10 footprints, respectively, from each foot, and we located specific dot pairs (7, 12, and 5, respectively) from the same row in each footprint. We used 2 sources of multiple footprints made by the same foot of wild fishers in California (Zielinski et al. 2004a) and in New York (Gompper et al. 2006), USA.

Field Trials

At each field site we marked a transect along hiking trails and unpaved roads. All trails were spaced far enough apart (>5 km) that the likelihood of a single individual fisher visiting stations >1 trail would be very low. We positioned a series of 6 baited, covered track plates with 500-m spacing along 3.5-km transects during summers of 2000-2002 (Gompper et al. 2006). Stations were set for 12 days, and we checked them every 3 days to replace baits and contact paper as needed. We applied soot to aluminum plates with a portable kerosene lantern made from a paint can. We attached contact paper to the baited end of the aluminum plate to collect foot prints. We digitized fisher footprints from each transect that exhibited sufficient quality with a computer scanner and compared them to each other. All animal research followed guidelines established by the American Society of Mammalogists (American Society of Mammalogists Animal Care and Use Committee 1998) and was approved by the Wildlife Conservation Society Animal Care and Use Committee and the New York State Department of Environmental Conservation permitting office.



Figure 4. Distribution of spacing between 2 adjacent dots from the same row, measured on the left and right forefeet of 10 fishers. We took measurements from Adirondack fisher specimens at the New York State Museum, New York, USA.

RESULTS

Footprint Uniqueness and Repeatability

We could almost always identify high-quality prints from the same animals by their dot patterns (Fig. 3). In our tests with prints collected in the field, 2 examiners missed one match of high-quality prints (34 of 36 correct, 94%). Of the 4 fair-quality triads, examiners missed an average of 1.3 matches (24 of 36 correct, 67%).

Using a bin size of 0.06 mm (3 SD of the variation of dot pairs among multiple prints of the same foot), 35.43% of 1,400 intra-dot measurements on prints from museum specimens fell into the most common size bin (0.22-0.28 mm; Fig. 4). Thus, the most likely pattern would have this spacing between dots in a row. Assuming nearby spacing distances were independent, the probability of encountering a series of dots with any given spacing configuration is $P_n \leq$ 0.35^n (eq 2). The correlation coefficient of spaces between 3 neighboring dots of the same row (0.30) was significant (statistical power = 0.92 for $\alpha = 0.05$) but only had mild explanatory value (proportion of explained variance $r^2 =$ 0.09). Solving equation 1 for n suggests that making 306 measurements of spaces adjacent to dot pairs that were of the most common spacing would result in approximately 107 measurements that would fall within the most common range of 0.22-0.28 mm (Fig. 4). We found 108 measurements, suggesting no autocorrelation in dot spacing within the same row, and the suitability of equation 2 to estimate the probability of occurrence of a dot pattern.

Dot pairs reproduced with consistent patterns across multiple prints made by the same foot. The standard deviation of spacing for any given dot pair from prints made by museum specimens varied from 0.01 mm to 0.03 mm. This variation was roughly an order of magnitude smaller than variation between different dot pairs within a footprint (Fig. 4), suggesting dot patterns are reliable markers to recognize individuals.

Matching Footprints from Free-Ranging Fishers

We recorded multiple fisher detections from 10 transects providing 62 sheets of contact paper displaying ≥ 1 fisher footprint, of which 85% yielded footprints of high or medium quality such that we could match them (Table 1).

Table 1. Application of print matching to identify individual fishers responsible for tracks collected at 10 sites, each with a transect of 6 track plates spaced at 500-m intervals, run for 12 days. Data were collected over the summers from 2000–2002 in the Adirondack region of New York, USA. We defined detections as ≥ 1 fisher tracks on the contact paper among 4 checks of the stations.

Site	Fisher detections	Detections with usable prints	Estimated no. of individuals
1	2	0	1
2	2	2	1
3	6	3	1
4	3	3	1
5	3	3	1
6	3	3	1
7	4	2	1
8	10	10	2
9	14	12	1
10	15	15	2
Total	62	53	12

We deemed matching possible when footprints from different sheets contained distinct dots in similar areas of the metacarpal pad. We found most (typically 100%) matchable detections on any given transect to exhibit similar dot patterns, with ≥ 10 dots to correspond between 2 footprints, corresponding to a maximum probability for a false match of approximately 0.00003. Only 2 of 10 transects produced footprints determined to be from >1 individual, and in both of those the second individual only visited once. Although the number of fisher detections ranged from 2 to 15 per site, we determined that just 1–2 individuals at any site were responsible for these track-plate visits.

Good-quality prints from the same individual were more difficult to match if the pattern was distorted because of differences in presentation of the foot on the tracking surface. The most common type of distortion, caused by reduced weight on the foot and less spreading of the pad, resulted in compression of dots along the print's length (Fig. 5). Although the spacing was not exactly the same, dot features still corresponded between 2 images.

DISCUSSION

We found that individual fishers could be recognized from footprints made at enclosed track-plates, as suggested by Foresman and Pearson (1998). With >1,000 dots typically present in a fully detailed fisher metacarpal pad print, the probability of occurrence of 2 similar prints by chance alone is small. Our model showed that the probability of a false match decreased exponentially as more dot features are matched, demonstrating that partial prints typical of field work are still useful. For example, matching only 5 dot pairs results in a 0.005 maximum probability of a false match (eq 2), whereas 10 matching pairs reduces the probability to 0.00003.

Empirical tests produced less optimistic results, making mistakes in 2 of 36 best-quality print matches and 12 of 36 fair-quality matches. However, this test is not completely realistic because we forced examiners to make a match even



Figure 5. Two prints from the left front metacarpal pad of the same freeranging fisher showing slight distortion in the print pattern: A) typical print; B) compressed print.

on the most difficult prints. In field situations, the most difficult prints may be deemed un-usable. Furthermore, most test subjects had no print matching experience past our online tutorial. The 4 subjects with more experience missed, at most, only the most difficult print.

Equation 2 assumes the examiner attempted to match footprint portions located in exactly the same part of the metacarpal pad. This is somewhat unrealistic, resulting in some increase in the probability of a false match over model estimates. However, this is offset because the simplifying assumptions of our model tend to make predictions conservative. More rigorous estimation of the probability of falsely matching footprints would be complicated. Indeed, a similar question regarding human fingerprint matching criteria has yet to be thoroughly resolved despite intense effort by many researchers (Cho 2002, Pakanti et al. 2002). We argue that our calculations approximate the true odds and give guidance as to how many dot pairs need to be matched in partial prints. Data on the ranging behavior of fishers also helps determine how many dots need to correspond between footprints to conclude they were made by the same individual. Given the strong intrasexual territoriality of fishers (Powell 1979, Arthur et al. 1989), their typical home range size (approx. $20-90 \text{ km}^2$ for M, 8–40 km² for F; Powell and Zielinski 1994, Zielinski et al. 2004b), litter sizes of 2–3 (Powell 1993), and the presence of transient or dispersing animals on the landscape, we expect the number of animals that could be responsible for a footprint collected from nearby (<5 km) track-plate stations to be on the order of 10. Thus, matching even as few as 10 dots between footprints should be sufficient to conclude a single fisher made the 2 prints.

Applying the Technique to Field Data

The practicality of using this technique on wild fishers will depend on recognizing ≥ 1 footprint from the majority of visits to a track plate by the same individual. In this regard, results from analyzing the Adirondack track plates were encouraging as most (85%) of the visits resulted in matchable footprints. Anecdotal observations have found that dry conditions provide better quality prints (R. Kays and C. Herzog, New York State Museum, unpublished data), suggesting this technique would be best applied in arid areas or seasons.

Because previous studies have been unable to distinguish the individual responsible for track-plate visits, researchers have been conservative in data analysis from nearby track stations and assumed they were not independent events (Zielinski 1995, Hamm et al. 2003). Our analysis of data from along a trail suggests these assumptions were accurate since a single animal was responsible for most track-plate visits to our 6 track stations spaced every 500 m. We expect more individuals were using the area surveyed but were not detected. Longer surveys and nonremovable bait (i.e., scent lures; Loukmas et al. 2002) would probably increase the number of individuals detected.

Because the morphological structures on the foot pads are present in a wide variety of species (Whipple 1904), the fingerprinting method described here has the potential to be applied in other species. From our experience with Adirondack mammals we found prints of weasels (*Mustela* sp.) and American marten (*Martes americana*) have similar patterns to fishers, but would be challenging to match because their feet are so small, and their weight so slight, that few dots are available for matching. Larger animals, such as striped skunk (*Mephitis mephitis*), Virginia opossum (*Didelphis virginianus*), raccoon (*Procyon lotor*), and porcupine (*Erethizon dorsatum*), have larger, heavier feet and leave darker prints that have a greater chance of being matched using this method.

Practical Issues in Footprint Processing and Storage

It is common practice to store footprints by inserting the shelf-paper into clear plastic document protector sleeves. If prints are to be used to identify individuals, care must be taken to ensure that shelf-paper does not become wrinkled or bubbled when inserting it into the document protector sleeve to preserve all pattern details. We suggest it is better to photograph prints in the field with a high-resolution digital camera (≥ 4 megapixels) before storing sheets. A suitable camera should have sufficient close-focusing capability that the entire frame can be filled with the metacarpal pad (approx. 2.5 cm). All images should be recorded at the same scale using a stand for the camera or have a ruler in the photograph.

Manual Versus Automated Pattern Matching

In the process of teaching this technique to others, we learned that some biologists have more aptitude than others for spatial pattern recognition and matching, a fact long recognized by those hiring criminal fingerprint technicians. Before using this method it is important that technicians get appropriate training and their matching aptitude is evaluated. We have developed an online tutorial for this purpose (http://www.nysm.nysed.gov/research/biology/fisher/index. html). Additional practice should be performed on tracks collected from the field, assuming multiple prints from the same track-event are from the same individual.

The limited number of prints generated from any practical study means manual print comparison is practical. However, the objectivity and speed of an automated computer printmatching tool is desirable. We tested fisher print matching with several automatic human fingerprint identification systems, including commercial packages and those used by the New York State Division of Criminal Justice Services. The best programs could eliminate the most different prints, but generally could not identify and link the dot features, especially with smudged prints. This is not surprising because these systems are almost exclusively designed to identify and match points of minutia (points where human fingerprint ridges either end or bifurcate), not dots. Although papillae on fisher foot pads form apparent rows, fisher feet lack the true ridges associated with human fingerprints.

It is probable that specialized software could be developed to aid in matching fisher footprints (e.g., Krijger 2002, Arzoumanian et al. 2005). This could be based on interpreting prints as patterns of dots rather than ridges. Although it seems unlikely such a system would rival an experienced human for matching low-quality images, it might prove useful in narrowing the search to fewer candidate prints, a common application of these automated tools in the field of human fingerprint analysis.

MANAGEMENT IMPLICATIONS

Our fingerprint identification method provides a new tool to estimate the density of fishers, and perhaps other species, over large areas with less labor. At a minimum, the number of unique tracks would represent the minimum number of animals. Multiple track collection (capture) events could also provide data for a more precise estimate using markrecapture analysis across independent sample events (Nichols and Dickman 1996). Other advantages of this method include the relative permanence of the pad patterns (in contrast to conventional ear tags; York 1996), the relative lack of stress affecting behavior and movements of target species, and the ability to cover larger areas with the same field effort because track-boxes do not need to be checked daily. Finally, track plates could provide useful data on other carnivore and small mammal species in the area (Zielinski 1995, Glennon et al. 2002, Gompper et al. 2006).

ACKNOWLEDGMENTS

Funding for this work came from the Wildlife Conservation Society, Geraldine R. Dodge Foundation, National Geographic Society, Columbia University, University of Missouri, New York State Museum, and the National Science Foundation (DEB 0347609). The Albany Pine Bush Preserve Commission, Adirondack Park Agency, New York State Department of Environmental Conservation, the Rosamond Gifford Zoo, and Saratoga National Historical Park provided permitting and logistic support. Field and laboratory work benefited from the assistance of J. Bopp, C. Doyle, P. Dwyer, A. Fox, C. Hass, E. Hellwig, J. Isabelle, S. LaPoint, N. Korobov, H. Krijger, T. LaBarge, J. Malcolm, J. Richardson, D. Ruggeri, and D. Taylor. In addition to 3 of the authors, J. Bopp, P. Gelok, T. Kirk, J. Loukmas, M. Toscano, and S. LaPoint took the time to learn the technique and take the matching test, for which we are grateful. Numerous private landowners generously gave permission to conduct surveys, including the Adirondack League Club, International Paper Company, The Nature Conservancy, Brandreth Park, Ross Park, Domtar Industries, Gulf View Hunting Club, Miner Agricultural Institute, and the Dragoon and DeCosse families. We thank P. Kernan at the New York State Museum for her illustrations.

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Associate Editor: Whittaker.