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Validation of a rigorous track classification technique: identifying individual mountain lions

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Abstract

Despite track survey efforts, the inability to identify individuals from survey data impedes accurate density estimates and density indices for large carnivore species. We present a track classification method for mountain lions *Puma concolor* using discriminant function analysis that improves and validates the method presented in Smallwood and Fitzhugh (1993) (Smallwood, K.S., Fitzhugh, E.L., 1993. A rigorous technique for identifying individual mountain lions *Felis concolor* by their tracks. Biological Conservation 65, 51–59) and further discussed in Grigione, Burman, Bleich and Pierce, 1999 (Grigione, M.M., Burman, P., Bleich, V.C., Pierce, B.M., 1999. Identifying individual mountain lions *Felis concolor* by their tracks: refinement of an innovative technique. Biolkogical Conservation 88, 25–32). Artificial tracks, made from molded casts of the feet of 13 lions, were used to simulate variability from field conditions in a controlled laboratory setting. We tested the effects of multiple track recorders and two soil depths on linear and angular measurements of the entire paw and shape measurements of the heel-pad. We identified six track measurements that correctly matched 96% of track tracings to known individual mountain lions, even with variability from multiple track recorders and soil depths. Model validation, performed on lab and novel field data in which the number of individual mountain lions was unknown, illustrates the efficacy of the method. Following the field-based study by Smallwood and Fitzhugh (1993), this study provides support for the utility of the discriminant analysis method for track data and outlines future application of this method to field data. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Discriminant analysis; Puna concolor; Individual identification; Mountain lion; Puma; Cougar; Track classification; Carnivore density estimates

1. Introduction

Managing and conserving carnivore populations depends on reliable methods of monitoring population trends. Because of the challenges associated with locating and directly handling carnivores, many researchers have explored indirect methods of assessing carnivore densities (Kutilek et al., 1983; Van Dyke et al., 1986; Van Dyke and Brocke, 1987; Karanth, 1987; Becker, 1991; Smallwood, 1994; Smallwood and Fitzhugh, 1995; Zielinksi and Truex, 1995; Foresman and Pearson, 1998; Sargeant et al., 1998). These studies use animal sign (e.g. tracks or feces) as indices of abundance and distribution within a given area, quickly and inexpensively. However, the ability to identify individuals from animal signs remains problematic (Panwar, 1979; Gore, 1993; Smallwood and Fitzhugh, 1993; Das and Sanyal,

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1995; Karanth, 1995; Riordan, 1998; Grigione et al., 1999; Zalewski, 1999; Grigione and Burman, unpublished manuscript, but see Ernest et al., 2000). In addition to mountain lions, these authors have attempted to develop track classification techniques for tigers (*Panthera tigris*), snow leopards (*Pathera uncia*), and pine martens (*Martes martes*). A similar approach has also been adopted for track identification of black rhinoceros (*Diceros bicornis*, Z. Jewell, personal communication). Thus, although this study focuses on mountain lions, the importance of the basic technique of track identification applies to a larger number of difficult-to-study species.

Recent studies (Smallwood, 1997; Smallwood and Schonewald, 1998) suggest that mountain lion density indices derived from track surveys may overestimate actual densities as a result, in part, of survey biases towards areas in which animals are known to occur. One solution to this is to randomly survey for lions throughout an area of interest. Track surveys can be randomized over large areas, but require substantial

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time and personnel. Data from such surveys (Smallwood, 1994; Smallwood and Fitzhugh, 1995) are limited to the number of transects included and the total number of tracks found. If individual lions could be determined based on tracks, survey precision would improve. However, a reliable and powerful method that can identify individual mountain lions from tracks has not been fully developed.

The development of a method to reliably identify individual mountain lions from track data has been hampered by (1) the few track sets and tracks per track set that field surveys typically yield, and as a result (2) a minimal ability to determine track measurements that allow for individual differentiation. Although variation in field conditions, like multiple track recorders and soil depths, is believed to impair lion identification methods, it is impossible to test the effects of these field conditions without sufficient track replications (Gore et al., 1993; Smallwood and Fitzhugh, 1993; Riordan, 1998; Grigione et al., 1999; Grigione and Burman, unpublished manuscript). Field data from track or radio-collar surveys may also be limited by an inability to positively link a track to an individual lion due to home range overlaps (Smallwood and Fitzhugh, 1993; Grigione et al., 1999; Zalewski, 1999). Smallwood and Fitzhugh (1993) were able to assign 92% of tracks from a track survey to putative individual lions, but due to small sample size were unable to test for the impact of track recorders and soil depths, or to determine the most powerful track measurement variables. However, the identity of each lion could not be verified; these authors assumed each track set was made by an individual lion because of substantial geographic distance between track collection sites. Subsequent studies have also been unable to systematically test or improve classification methods, in part, due to insufficient track replications from known individuals (Grigione et al. 1999; Riordan 1998).

We use tracks generated in the laboratory from known individual lions to determine the most effective track measurement variables, and the effect of multiple track recorders and soil depths on individual mountain lion identification. Using this laboratory-generated track database, we propose a combination of track measurements that can be used to identify individual mountain lion from unclassified track sets. We determine the variation created by two soil depths and five track recorders, and we assess the impact of this variation on track measurements and, ultimately, on the identification method. To test method efficacy, we performed a validation test on unused lab track tracings, using a double blind experimental design. We then tested the method on an independent field data set. This study also demonstrates the feasibility of using an image measurement computer program once a track has been traced in the field.

2. Methods

We made plaster casts from the rear, right foot of 13 mountain lions. Eleven of the 13 lions were killed under depredation permits from the California Department of Fish and Game taken from six locations in two counties in California. This depredated sample included 10 males and one female, ranging in age from 2–7 years. Plaster casts were then used to create a silicone mold with the same dimensions as the actual foot. Two other silicone molds were made directly from tracks in soil; one mold was from another county in California and the second was from Florida. A *mold* refers to a complete replica of the lion paw, including the heel pad and four toes.

2.1. Track generation

We created a mold imprint by pressing molds into sandy loam soil, 67% clay, 23% silt, 10% sand (Gee and Bauder, 1979), that was spread on a rectangular pan and leveled to two depths — deep (\geqslant 7 mm) and shallow (1–3 mm). Five track recorders then measured the mold imprint, the track.

Fitzhugh trained all track recorders in track measurement protocol (Fjelline and Mansfield, 1989) prior to data collection. To ensure that all recorders maintained the same protocol and techniques throughout the study, each recorder traced the same practice track and compared tracings among recorders at the start of each measurement session. All five recorders traced all 13 tracks during each measurement session. The order in which the tracks were traced was randomized for each session. Each track was made seven times in deep soil and eight times in shallow soil over approximately a 2month period. The five recorders traced each track on acetate sheets, which rested on glass plates raised approximately 8 mm above the imprints. The traced outline included the entire track — the heel pad and four toes.

2.2. Track data

Using the 13 molds, we generated 797 track tracings. We analyzed subsets of these data to investigate the discriminatory ability of seven linear/angular measurements (Fig. 1), and 10 shape measurements (see Appendix). These 17 measurements describe dimensions of the entire paw or heel pad.

To find the fewest number of track measurements that maximized individual discrimination while allowing the method to be applied to smaller data sets, we selected the measurement variables from the separate linear and shape analyses that classified the highest number of track tracings into known groups. From these two analyses, we selected six measurements, three linear and three shape. These measurement variables were selected

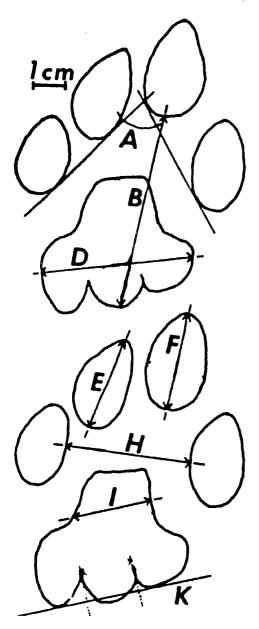


Fig. 1. Linear and angular measurements that describe the entire paw (from Smallwood and Fitzhugh, 1993). A, angle between toes (ABT); B, heel to lead toe length (HLTL); D, heel width (HW); E, third toe length (TTL); F, lead toe length (LTL); H, outer toe spread (OTS); I, midline width (MW), a line parallel to and 25 mm from the baseline (see K); K, baseline used to draw midline. These measurements were used in Smallwood and Fitzhugh (1993) and are similar to those used by Grigione et al. (1999). Measurements were made directly from the acetate tracings to 0.5 mm and 1° precision using standard rulers and protractors.

based on the absolute magnitude of the standardized discriminant function coefficients, accounting for correlations among measurements (Section 2.5.).

We then tested the classification method with these six measurements on a small sample of unused lab-generated track tracings. To provide an independent test of the classification method, we then tested the method on field data collected in two different counties from our depredated lions. These field data included tracings of the rear, right paw from five track sets taken from five locations. Each track set had four track tracings. Smallwood made the tracings directly over the track using the same protocol as our track recorders.

2.3. Statistical analysis

This track classification and identification method uses discriminant function analysis (DFA). Typically, DFA is used to determine the variables that best categorize data into two or more known groups. Thus, a traditional DFA uses the discriminant equation to yield a suite of predictor variables that can correctly classify the highest percentage of the data into known categories (Tabachnick and Fidell, 1983). In addition to using the discriminant equation to yield predictor variables that maximize data classification into known groups, we then use these known predictor variables to generate groups of individual lions in unclassified data sets. Thus, we employed two separate statistical procedures. First, we identified the most effective linear and shape track measurement variables that separate known tracks into distinct groups using DFA. We then used this known measurement variable combination on uncategorized lab and field data in a second DFA.

All data were analyzed using STATISTICA (StatSoft, 1984) and were tested for normality, outliers, multicollinearity of predictor variables, and homogeneity of variance-covariance matrix using Box's M test.

2.4. Impact of multiple recorders and soil depths

To test the impact of multiple track recorders and soil depths on our method, we performed multivariate analysis of variance (MANOVA) on all the track measurement variables. To test whether potential statistical significance was a result of the large number of track tracings, we evaluated the effect sizes of both multiple recorder and soil depth. To do this, we used a MAN-OVA-type model to examine the amount of variability described when incorporating the effect of different, individual lions alone, both different lions and multiple track recorders, or both different lions and soil depths. We created a three-dimensional vector derived from the first three canonical discriminant eigenvectors from the track measurement variables in each analysis and used this resultant vector as the dependent variable (Johnson and Wichern, 1988). We compared the variability explained by three models: (1) a model incorporating the effect of different individual lions alone; (2) a model with the effects of different lions and multiple track recorders; and (3) a model with the effects of different lions and soil depths. These MANOVA models, constructed to test effect size for multiple recorders and soil depth across predictor variables, were evaluated based on the coefficient of determination (R^2) values. R^2 values were calculated using the standard Euclidean distance between vectors. Euclidean distance between any two vectors is calculated as:

Distance between vector u and vector $v = \sqrt{(u-v)'(u-v)}$

where (u-v)' represents the transpose.

2.5. Variable selection

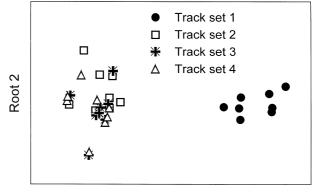
We used the absolute magnitude of the standardized discriminant function coefficients, accounting for correlations among measurements, to determine the relative importance of predictor variables to the linear and shape classification functions (Tabachnick and Fidell, 1983). Correlated, or redundant, predictor variables were eliminated to avoid matrix ill-conditioning. We also evaluated the variables' sensitivity to multiple recorders and soil depths (Section 2.3.). Our goal was to find the fewest number of uncorrelated predictor variables that maximized individual discrimination, making the method applicable to smaller data sets. DFA assumes a maximum of n-2 predictor variables, where n is the number of data cases in the analysis (Tabachnick and Fidell, 1983).

2.6. Method application: how it works

Once measurement variables are identified that best classify the data into known groups, it is possible to apply this method on unclassified data in which the number of individual lions is not known. To apply this method to new data, each track set is assumed to represent a discriminant group. By evaluating the *P* values from the squared Mahalanobis distances between the group centroids, the Wilks' lambda values, the classification matrices, and the scatterplot of the first two discriminant roots (Fig. 2), the assumption that each track set is from a different lion is judged to be true or false.

2.7. An example

In the example in Fig. 2, the DFA was performed with four track sets as the grouping variables and the six combined track measurements as the predictor variables. As is evident from the scatterplot, track set 1 is distinct from the other three track sets and thus, is a putative individual lion. Track sets 2–4, however, have considerable overlap and require additional investigation. The next step is to make pairwise and three-way comparisons of the *P* values associated with the distances between groups, the classification matrices, and



Root 1

Fig. 2. A scatterplot of the discriminant functions illustrates pairwise and three-way comparisons necessary to distinguish track sets, which may represent the same lion. Here, track set 1 is clearly an individual lion. After additional analysis, track sets 2–4 were found to represent the same lion.

the Wilks' lambda values. The pairwise and three-way comparisons of these values on track sets 2–4 concur with the trend suggested in Fig. 2; indeed, track sets 2–4 all come from the same lion.

2.8. Model validation

We used lab and field data to test the method on unclassified, or non-categorized, data in which the number of individual lions is unknown a priori. For the first validation test, previously unused lab data (177 track tracings) were divided into 72 groups. Each group had four track sets representing two to four different lions. A track set is multiple track tracings that come from the same lion. To create the track sets, we randomly sampled without replacement all track tracings from an individual lion, including tracings from both soil types and all recorders. The four tracks sets used in each of the 72 groups were also randomly chosen using a double blind experimental design such that the number of individual lions represented by the four track sets (two to four lions) was known only to the data sampler not the data analyzer.

Previous track analyses have suggested that at least four tracings should be used per track set (Smallwood and Fitzhugh, 1993; Zielinski and Truex, 1995; Grigione et al., 1999). We used the lab data validation test to evaluate the effect of the number of tracings per track set. We created track sets that contained four, six and eight track tracings. The double blind method was used to create 24 groups for each track set size (four, six, and eight track tracings per track set) to yield a total of 72 groups.

A similar protocol was used to test the classification method on a field data set collected in Northern California in 1987 by S. Smallwood. These data included 20 track tracings from five track sets. All tests had two to four individual lions represented with four tracings per

track set. Due to the limited number of track sets and tracings per set, we were unable to test the impact of tracings per track set on the field data.

3. Results

3.1. The impact of variability from recorders and soil depth

MANOVA suggested that multiple recorders and soil depth did influence the track measurement variables that best classified the data into known groups (Table 1). As seen in Table 1, there are statistically significant differences in means among track recorders and soil depths for several track measurements. However, the MANOVA models constructed to test effect size for multiple recorders and soil depth across predictor variables indicated that the percentage of variability accounted for by models with or without multiple track recorders or soil depths are similar (Table 2). Thus, although the standard MANOVA models suggest that recorder and soil depth effects are significant for some individual track measurement variables, their overall effects on the combination of track measurements appear to be negligible.

3.2. Measurement variable selection

Six measurements, three linear and three shape, were chosen as the most powerful suite of track measurements (Angle between toes, Outer toe spread, Heel to lead toe length, Perimeter, Shape factor, Major axis length) based on the absolute magnitude of the standardized discriminant function coefficients, accounting for correlations among measurements, and their sensitivity to multiple track recorders and soil depths (Table 3).

The discriminatory ability of the measurement variables from all data was evaluated by the percentage of tracks correctly classified or grouped by an individual lion. Linear and angular variables result in better classification of individual tracks than did shape measurements, but the two types of measurements combined were superior to either type alone (Table 4). Shape variables performed better in shallow soil, whereas linear/angular variables performed better in deep soil. The percentage of tracks correctly classified by both linear and shape variables was higher for tracks in deep soil (97.4%) and dropped slightly for shallow soil tracks (93%).

3.3. Model validation

The results from the lab validation tests suggest that the six track measurements we present consistently and correctly discriminate individuals from a data set of unclassified lions. This method identified the correct number of lions in 96% of the lab track groups; in three out of the 72 track groups the number of individual

Table 1 Multivariate analysis of variance results with effects of multiple track recorders and soil depths on combined linear and shape measurements

Variable	Effects	Type III M.S. error	M.S. error	F (d.f. 1, 2)	P
Angle between toes	Recorders	32.72	10.23	3.20	0.01
	Soil depth	0.516	10.23	0.05	0.82
Heel to lead toe length	Recorders	152.73	7.78	19.55	0.00
	Soil depth	5.90	7.79	0.76	0.38
Outer toe spread	Recorders Soil depth	96.78 56.35	2.81 2.81	34 20.05	0.00
Major axis length	Recorders Soil depth	687.99 111.87	9.72 9.72	70.75 11.5	0.00 0.01
Perimeter	Recorders Soil depth	95.24 6361.71	179.18 179.18	53.15 35.50	0.00
Shape factor	Recorders Soil depth	0.34 0.003	0.003 0.003	114.96 1.12	0.00 0.29

M.S., mean square.

Table 2
Evaluation of the effect size of multiple recorders and soil depths on track measurement variables on linear, shape, and linear and shape measurements

	Evaluating effect size coefficient of determination (R^2) values ^a Main effects included in model				
Data	Lion only	Lion-recorders	Lion-soil depths		
Linear	0.898 0.551	0.903 0.601	0.898 0.564		
Shape Linear and shape		0.967	0.966		

a R² values represent the amount of variability described by each of the models when incorporating the effect of different individual lions alone, the effect of both different lions and multiple track recorders, or the effect of both different lions and soil depths.

lions was misidentified. There was no difference in classification errors between track groups with four, six, or eight tracings per track set. The model validation tests indicate that even with small data sets in which the number of lions is not known a priori, the method performs well in correctly identifying individual lions. The classification method was equally effective in identifying individuals using the unclassified field data. In nine of 10 track groups, the correct number of individual lions was identified.

4. Discussion

4.1. Discriminatory ability

The discriminant analysis method we present is more effective at identifying individual lions by their tracks

Table 3
Selection of track measurement variables was based on the absolute magnitude of the standardized discriminant function coefficients for Root 1 and Root 2 of the discriminant function analysis for the linear and shape analyses^a

	Standardized function coefficients		
Linear measurements		Shape Measurements	_
Outer toe spread (OTS)	0.94	Shape factor	2.1
Heel to lead toe length (HLT	Major axis length	1.3	
Angle between toes (ABT)	0.68	Perimeter	1.3
Third toe length (TTL)	0.25	Area	1.1
Heel width (HW)	0.19	Minor axis length	1.1
Lead toe length (LTL)	0.16	Compactness	0.98
Midline width (MW)	0.15	Major axis slope	0.52
		Center of mass, X	0.37
		Center of mass, Y	0.14
		Minor axis slope	0.11

^a We also accounted for correlations among measurements, and sensitivity to multiple track recorders and soil depths. Only six of the 17 measurement variables were used, in bold italics, to maximize the discriminatory ability of the method and ensure method applicability to smaller data sets.

Table 4
The percentage of tracks correctly classified into known groups using discriminant function analysis on linear, shape and a combination of track measurements^a

Track measurements	% Correctly classified			
	Complete data set	Shallow soil	Deep soil	
Linear	89.9	89	92.3	
Seven variables	(620)	(327)	(293)	
Shape	75.3	83.3	67.5	
Ten variables	(473)	(234)	(239)	
Linear and shape	96.2	93.3	97.4	
Six variables	(239)	(119)	(120)	

^a The number of track tracings used in each analysis is shown in parentheses.

than any technique to date. We identified a combination of six track measurements that correctly matched 96% of the lab-generated tracks into known groups of individual lions. Using two smaller, unclassified data sets, with lab data and then with independent field data, we tested this method using a DFA in which the number of individual lions in each analysis was unknown to the data analyst. The DFA method also performed well on the unclassified field data.

4.2. Track measurement variables

Although there are potentially an infinite number of track measurements from which to choose, the measurement variables chosen here for the most effective analysis describe relevant, non-overlapping dimensions of the entire paw and heel pad. Thus, the variables have biological meaning as well as effective discriminatory ability.

The variables are also robust to the effect of multiple track recorder and soil depths. Although recorder and soil depth did influence some predictor variables independently, when linear and shape variables were combined the discrimination of the models was not impaired by multiple recorders or soil depths. The results from the MANOVA models suggests that although there were statistically significant differences for individual measurements, the effect sizes of soil depths and multiple recorders have little practical significance for the suites of linear, shape, or linear and shape measurements we tested.

The analyses suggest that soil depth had a greater effect on track classification than recorder effects, particularly with heel-pad shape measurements. This finding is supported by previous work (Grigione and Burman, unpublished manuscript). Although these authors were not able to discriminate tracks in different substrates directly from the field or from the lab using shape analysis of the rear outline of the heel-pad, we have found that measurements of the entire heel-pad can help to discriminate among track sets. Although heel-pad shape variables alone classified only 75.3% of tracks correctly, when combined with linear measurements, the shape measurements substantially increased disthe criminatory power of the method, resulting in 96% correct classification of tracks. In addition, the increase in the percentage of tracks correctly classified in the combined measurement analysis is noteworthy as it was obtained despite a large reduction in sample size (239 vs. 797 track tracings) and fewer predictor variables.

4.3. Computer aid

Like other recent track identification work (Riordan, 1998; Grigione and Burman, unpublished manuscript), this method used both hand measurements and computer digitization. The computer program we used, SigmaScanPro-4TM, created accurate measurements easily and quickly. The effect of multiple digitizers had no effect on any of the dependent, independent or interaction variables (Appendix). Although a calibration scale must be entered, it is feasible that all track variables, including linear, angular, and shape measurements, could easily be measured using the digitized track tracings.

Our findings suggest that a computer image measurement program increases the efficiency and accuracy of the method. The use of track photographs combined with image-measurement software may further increase method efficiency, by eliminating the need for track tracing (Grigione et al., 1999). Galentine and Fitzhugh

(1996) proposed a black box design that standardizes light and photographic quality of track images. Analysis is currently underway to test how effectively and accurately both linear and shape measurements can be made from these standardized photographs using SigmaScan Pro-4TM.

4.4. Application of the method

The application of a supervised classification method, like discriminant analysis, to field-generated data sets of unknown individuals has been criticized because of the need for a priori knowledge of individuals (Riordan, 1998; Grigione at al., 1999; Grigione and Burman, unpublished manuscript). However, as outlined in Smallwood and Fitzhugh (1993) and illustrated here, this method can be used effectively for track sets with no prior knowledge of the number or identity of individual lions. Using the measurement variables we present, it is possible to accurately classify mountain lion individuals given adequate tracings per track set (≥ 4). We tested this method on an unanalyzed portion of lab data in which the number and identity of lions per test was unknown and found that the method was highly effective in correctly classifying tracks — 96% of the tests yielded the correct number of individual lions. It is important to note that the validation test we performed on the laboratory tracks was biased against our method, as there were multiple recorders within track sets, which is highly unlikely in a field track survey setting. The method was also effective in classifying independent field data from a 1987 track survey.

The validation tests performed here were first steps in applying this method to complete track survey data. A large, track survey data set would potentially include other types of variation: flexibility of the live foot, variations in substrate topography, impact of speed of travel. different substrate types, and potential combinations of left and right tracks within a track set. Previous work provides some insight into the effects of this potential variation. Linear and angular measurements are most likely more sensitive to changes in live foot configurations than are heel-pad shape measurements. Nonetheless, using only linear and angular measurements, Smallwood and Fitzhugh (1993) were able to correctly match 92% of the tracks to individual lions with a field data set. Although the relatedness and identity of these lions was unknown, the track sets were found at distances that exceeded local movement of an individual mountain. In addition, Riordan (1998) demonstrated that six of the seven linear measurements we used showed little variability between left and right hind prints of other large carnivores. Thus, we expect our findings to be applicable to track survey data with only small changes to the discriminatory power of the method.

Because earlier work based on field observations of unknown lions required spatial separation to assume that different lions were sampled, a logical question is whether the method we propose can reliably discriminate among related, but different individuals. Eleven of the 13 mountain lion paw molds we used for this study came from lions in three areas separated by approximately 80–100 miles. Within each area, however, the collection region was only approximately 200 square miles. Thus, it is likely that there is a substantial degree of relatedness between lions in our study.

This general classification technique may also prove important for monitoring programs of other rare or cryptic carnivores. Our approach of using artificially created tracks from known individuals can provide a systematic method to evaluate measurement variables and field conditions without the limitations from small sample size representing few known individuals. Similar track measurements have been used with other carnivores in wild (Gore, 1993; Das and Sanyal, 1995; Zalewski, 1999) and captive settings (Riordan, 1998).

Several authors (Van Sickle and Lindzey, 1992; Beier and Cunningham, 1996; Smallwood and Schonewald, 1996; Smallwood, 1997) have outlined the problems of extrapolating mountain lion density from localized study areas to broader regions. One solution to this dilemma is to conduct randomized surveys over an entire region. This will require indirect population assessment methods, such as track surveys. If larger, less aggregated study areas need to be included to increase the accuracy of density estimates, as previous work suggests, an efficient and effective track identification method is necessary. While incorporating the variability inherent in field data, the discriminant classification method we present yields a higher percentage of correctly identified individual lions than any method previously proposed. Thus, the method can improve the relationship between track survey data and interpretation and, subsequently, lead to more accurate mountain lion population estimates than are now possible.

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Appendix. Heel-pad measurements as defined by Sigma Scan (SPSS Science, 1998)

These shape measurements were chosen to describe as many relevant dimensions of the heel pad as possible. Heel pad tracings were scanned and then were digitized using SigmaScanPro- 4^{TM} . Each image was calibrated with a known linear measurement (HW) applied to the same dimension in the digitized image. To ensure the digitization process did not introduce additional recorder bias, we included two new recorders who each digitized all the tracings in SigmaScanPro- 4^{TM} . These new recorders are referred to as digitizers. The effect of multiple digitizers was not significant for any of the independent variables or the interaction combinations (P values ≥ 0.98). All measurements are based on pixel number or (x, y) coordinate location.

Area, sum of the number of pixels defining the object. Center of mass, *X* and *Y*, the binary center of mass of an object is the geometric center. This measurement locates the *X* and *Y* coordinates of the geometric center. Where:

$$CM(X) = 1/n \sum_{i=1}^{n} X_i$$
 $CM(Y) = 1/n \sum_{i=1}^{n} Y_i$

n is the number of pixels in the object and X_i and Y_i are the coordinates of the ith pixel.

Compactness, numeric expression of the shape of an object as it moves from a circle to a line, defined as the perimeter squared, divided by the area. The minimum compactness of a perfectly measured and digitized circle is 4π . As an object tends towards the shape of a line, the compactness tends towards infinity.

Major and minor axis length, the *major axis* is defined by searching all the border pixels of an object and picking the two pixels that are farthest apart. The *minor axis* is drawn between two pixels defining the longest perpendicular line to the major axis. These points are defined by the endpoints of each of these lines: (MajX₁, MajY₁), (MajX₂, MajY₂) and (MinX₁, MinY₁) and (MinX₂, MinY₂).

The major and minor axes length measurements find the distances between the two endpoints defining the major and minor axes. Major axis length =

$$\sqrt{(MajX_2 - MajX_1)^2 + (MajY_2 - MajY_1)^2}$$

Minor axis length =

$$\sqrt{\left(\text{Min}X_2 - \text{Min}X_1\right)^2 + \left(\text{Min}Y_2 - \text{Min}Y_1\right)^2}$$

Major and minor axis slope, the angle of the major axis from a horizontal line

Major axis slope =
$$\frac{\text{atan}(\text{MajY}_2 - \text{MajY}_1)}{(\text{MajX}_2 - \text{MajX}_1)}$$

Minor axis slope =
$$\frac{\operatorname{atan}(\operatorname{Min}Y_2 - \operatorname{Min}Y_1)}{(\operatorname{Min}X_2 - \operatorname{Min}X_1)}$$

Perimeter, determined by the overall shape of the object and is measured along the diagonal edges of the object.

Shape factor, calculates how circular an object is. Where:

Shape factor =
$$\frac{4\pi \times \text{Area}}{\text{Perimeter}^2}$$

A perfect circle has a shape factor of 1.00 and a line has a shape factor approaching 0.00. Theoretically, the shape factor should never be greater than 1.

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