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A RIGOROUS TECHNIQUE FOR IDENTIFYING INDIVIDUAL MOUNTAIN LIONS *Felis concolor* BY THEIR TRACKS

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Abstract

We introduce a rigorous technique to make individual animal identification by tracks more objective than previously possible. With measurements from acetate tracings of two to six tracks from each rear foot of nine mountain lions Felis concolor, *multiple-group discriminant analysis accurately grouped 100% and 92% of the tracks from the left and right rear feet, respectively. From bootstrap analyses we concluded that mountain lion track set discrimination was best achieved with the spread of the outer toes, heel width, and the midline width of the heel pad. After further research, this technique can be used to improve population studies of mountain lions and other large animals.*

Key words: Mountain lions, *Felis concolor*, discriminant analysis, identification, tracks.

INTRODUCTION

Most large carnivores are sparsely distributed, cryptic, and difficult to study. Demand for information on mountain lion *Felis concolor* populations has increased recently, notably in California (Fitzhugh & Gorenzel, 1986; Mansfield, 1986). Mountain lion managers need information on population trends and distribution. Of those who tested and recommended track surveys for detecting trends in population size (Kutilek *et al.*, 1983; Fitzhugh & Gorenzel, 1985; Van Dyke *et al.*, 1986; Shaw *et al.*, 1988; Van Sickle & Lindzey, in press), nobody considered that individual mountain lions could be identified by their tracks. If individual mountain lions can be identified, then population estimates can be improved from track surveys, and capture and radio-telemetry studies.

People have for centuries tried to identify individual animals by their tracks, but few have tested the accuracy of their techniques quantitatively (Karanth, 1987). Hence, wildlife managers commonly believe tracking techniques are inaccurate. Researchers have discriminated tracks of individual mountain lions by using deformations and gross differences in size and shape (Currier *et al.*, 1977; Kutilek *et al.*, 1983; Fitzhugh & Gorenzel, 1985; Van Dyke *et al.*, 1986); by one or more track measurements (Koford, 1976; Currier *et al.*, 1977; Shaw, 1983; Fitzhugh & Gorenzel, 1985); by association with radio-telemetry locations (Fitzhugh & Gorenzel, 1985; Van Dyke *et al.*, 1986; Neal *et al.*, 1987); or by distances between tack sets (Currier *et al.*, 1977; Shaw, 1983).

Tracks from many mountain lions look so similar that even trained experts usually cannot discriminate them. In fact, we asked participants at the Third Mountain Lion Workshop in Prescott, Arizona (6–8 December 1988), to identify the three tracks in Fig. 1 that were from the same mountain lion foot (Table 1). We did not provide the respondents with all the information often available in the field (i.e. all the other tracks associated with those we presented), but neither would the respondents have known in advance how many tracks from a study area were from the same animal. None of 52 respondents discriminated all three tracks from the others, and the success rate for grouping two of the tracks did not vary with tracking experience of respondents. These results correspond with the inability of wildlife managers in India, who each had ≥6 years of tiger census experience, to identify any of four tigers represented by 33 track tracings (Karanth, 1987). A qualitative approach to track discrimination usually will not work. However, multiple track measurements should contribute a unique distribution of measurement values for each animal. Thus, the different measurement distributions can be used to identify individuals.

In this paper we report on a practical, quantitative technique to identify individual mountain lions by tracks of their rear feet. These data are difficult to collect, so data sets will be small. Therefore, we describe rigorous methods for making the most of the available information.

METHODS

Data collection

K. Shawn Smallwood surveyed dusty roads for mountain lion tracks in northern California mountain ranges during summer and fall 1987. A track is a single paw

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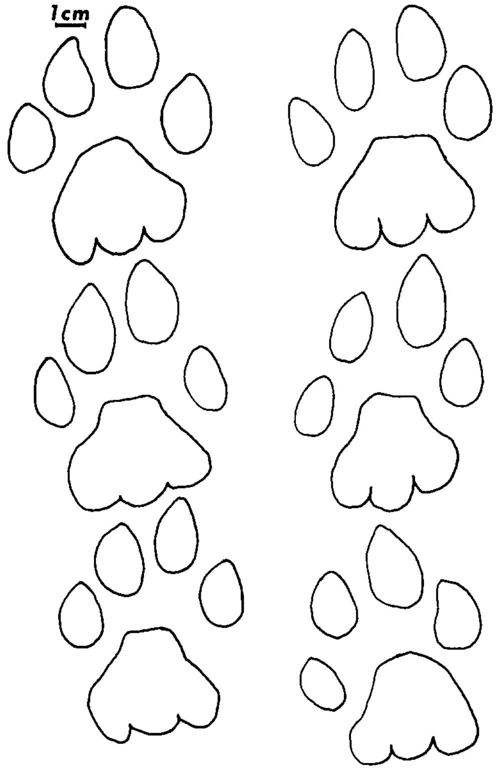

Fig. 1. Can you identify the three left rear tracks made by the same mountain lion? We use this illustration to show the difficulties in identifying mountain lions by their tracks. From four mountain lions, the three tracks in the right column were left by one, and the three tracks in the left column were left by three others. Measurements from these tracks were included in multiple group discriminant analysis and all tracks were correctly grouped.

print or tracing thereof, and a series of paw prints from the same individual is a track set. When Smallwood found mountain lion tracks in dust, he traced each track outline onto acetate sheets (after Panwar, 1979; Fitzhugh & Gorenzel, 1985; Fjelline & Mansfield, 1989), which took about 5 min per track. He recorded tracks from each rear foot two to six times on various slope gradients and soil depths available at each site (Table 2). Front tracks were recorded when possible.

Table 1. A mountain lion track discrimination test (Fig. 1) of participants at the Third Mountain Lion Workshop, Prescott, Arizona, 6–8 December 1988

	Respondents	Number and percent of respondents who chose two tracks from the one lion[a]
Total	52	12 (23%)
Biologists[b]	39	9 (23%)
Houndsman	4	1 (25%)
Had lion tracking experience	31	8 (26%)
Had no lion tracking experience	15[c]	4 (27%)

[a] No respondent chose the three tracks from the same track set, and 75% of all respondents chose tracks from three different track sets.
[b] The respondent holds a degree in wildlife biology or management.
[c] Six respondents failed to indicate whether they had experience.

To avoid mistaking tracks from two or more mountain lions as those from one individual, Smallwood only recorded tracks from the same distinct track set that he carefully followed along the road. Each track set recorded was ≥17·6 airline km from any other, and he surveyed on weekends during deer-hunting seasons when vehicles obliterated tracks quickly, sometimes while he recorded the tracks. He recorded tracks from nine mountain lions: one from the Mount Shasta area, three from the Georgetown Divide area of the Sierra Nevada, and five from the southern Mendocino National Forest in the Coast Range Mountains. All tracks were recorded within one day in the Georgetown Divide area, and within two days in the Mendocino National Forest. This combination of precautions made it unlikely that two track sets were recorded from the same mountain lion.

We used simple measurements (Fig. 2) that *a priori* appeared to possess little within-set relative to between-

Table 2. The slope and substrate conditions for rear foot tracks (left rear/right rear) used in the analysis

Location	Total tracks	Dust conditions			Slope of terrain in direction of travel					
		Light <2 mm	Medium 2–4 mm	Deep >4 mm	Level ground	Uphill			Downhill	
						<12°	13–25°	>25°	<12°	13–25°
Reynold's Basin[a]	4/4		4/4			3/3	1/1			
Goat Mt[b]	4/4	4/4			1/1		1/1	1/1	1/1	
Horse Mt[b]	2/2			2/2	2/2					
Little Round Mt[b]	3/5	2/5		1/0	1/1					2/4
Hull Mt[b]	4/4	4/4			4/4				1/1	
Alder Springs[b]	3/3		3/3		2/2				2/2	
Pollock Pines[c]	5/6		1/2	4/4	3/4				2/2	
Georgetown Divide[c]	4/4			4/4	2/2	1/1			1/1	
Balderston Station[c]	4/4	3/3		1/1	1/1				3/3	

[a] Mount Shasta area.
[b] Mendocino National Forest.
[c] Georgetown Divide area.

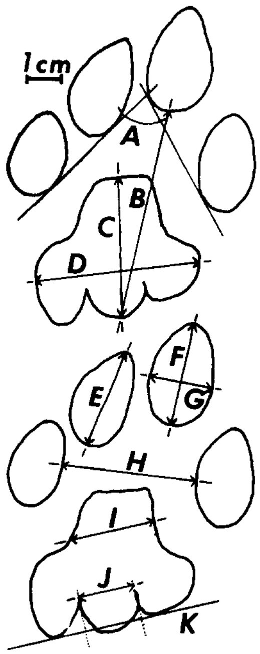

Fig. 2. Track measurements used to identify nine mountain lions: A, angle between toes (ABT); B, heel to lead toe length (HLTL); C, heel length (HL); D, heel width (HW); E, third toe length (TTL); F, lead toe length (LTL); G, lead toe width (LTW); H, outer toes spread (OTS); I, midline width (MW), a parallel line 25 mm from the baseline (see K); J, heel lobe width (HLW); and K, baseline used to draw midline.

set variation. Although we tried the heel length in our analyses, it varied greatly among tracks of any one individual and probably would not help discriminate individuals. Also, we tended to choose measurements with relatively large values, with the intent to minimize measurements and recording error relative to within-set variation. To minimize dependency, we avoided measurements that included part or all of other measurements. However, some unknown degree of dependency was inevitable among track measurements simply because most measurements correlate with foot size.

Smallwood used various angles and postures while tracing one right rear foot track eight times in the Georgetown Divide area to quantify recording and measurement error for that particular track. To compare recording error with the variation due to slope, he traced a total of six different tracks from the same foot for travel directed downhill, on level ground, and uphill. Variation due to slope was obtained by subtracting the recording error estimated from the single track (for this we assumed constant measurement error) from the total variation estimated from the six different tracks.

Statistics and analytical methods

We used the track measurements in Fig. 3 to determine if we could use multiple group discriminant analysis to identify individual mountain lions by their tacks. Discriminant analysis was described in an easily understood, practical way by Norusis (1985, pp. 75–116), and Seber (1984, pp. 279–343) described the multiple-group case as an extension of the two-group case. Our objectives were (1) to achieve optimal separation of track sets so that we could identify the measurements that best contributed to track set separation; and (2) to develop linear combinations of track measurements from known tracks to predict track set membership of unknown tracks. These objectives, respectively, are known as descriptive and predictive discriminant analysis (Williams, 1982, 1983; Afifi & Clark, 1984), and their linear models are known as canonical variates and discriminant functions, respectively. The statistical properties are the same for both analyses. In our case, the linear model takes the form:

$$\text{Track Set Membership} = a^*X_1 + b^*X_2 + c^*X_3$$

where X_1, X_2, X_3 are track measurements, and a, b, c are coefficients estimated to maximize track set separation.

With linear discriminant function analysis we assume that (1) the group distributions are normal with equal variances; (2) sample observations are independent; and (3) the sample observations are correctly classified. With continuous data, linear discriminant function analysis can tolerate some skewness, and is 'moderately robust to longer-tailed symmetric distributions and mixtures of normals' (Seber, 1984). It is 'satisfactory' for small departures from equal variance among groups, and initially misclassifying a portion of the groups has little effect on misclassification probabilities (Seber, 1984, pp. 299–300). Our sample sizes were too small to test for normality and equivalence of variances, but mountain lion track measurements are continuous morphometric data, which usually are normally distributed.

We used stepwise variable selection according to Wilks' lambda: the within-set sum of squares relative to the total sum of squares. With the stepwise procedure the measurement with smallest Wilks' lambda is entered into the model first. The measurement with the smallest Wilks' lambda among the remaining measurements (the first measurement already entered is not considered here) is entered second, and so on. After each variable entry, the model is examined for potential variable removal. Any variable will be removed if its tolerance (unique effect) is $<0{\cdot}001$. Stepwise variable selection maximize group separation while avoiding high correlation among the predictor variables.

We tried many combinations of measurements in Fig. 3 to achieve optimal track set separation. Model effectiveness was the percentage of tracks correctly grouped with their respective track sets. We also tested each measurement alone for its effectiveness to discriminate all nine track sets. Separate discriminant models were made of each foot, because no two feet are exactly the same size and shape for any one animal, and we wished to use as much of the available information as possible.

To estimate each measurement's contribution to track set separation, and at what point we could identify all mountain lions, we conducted eight separate analyses per rear foot with the eight measurements from the most effective models. (The eight-measurement model

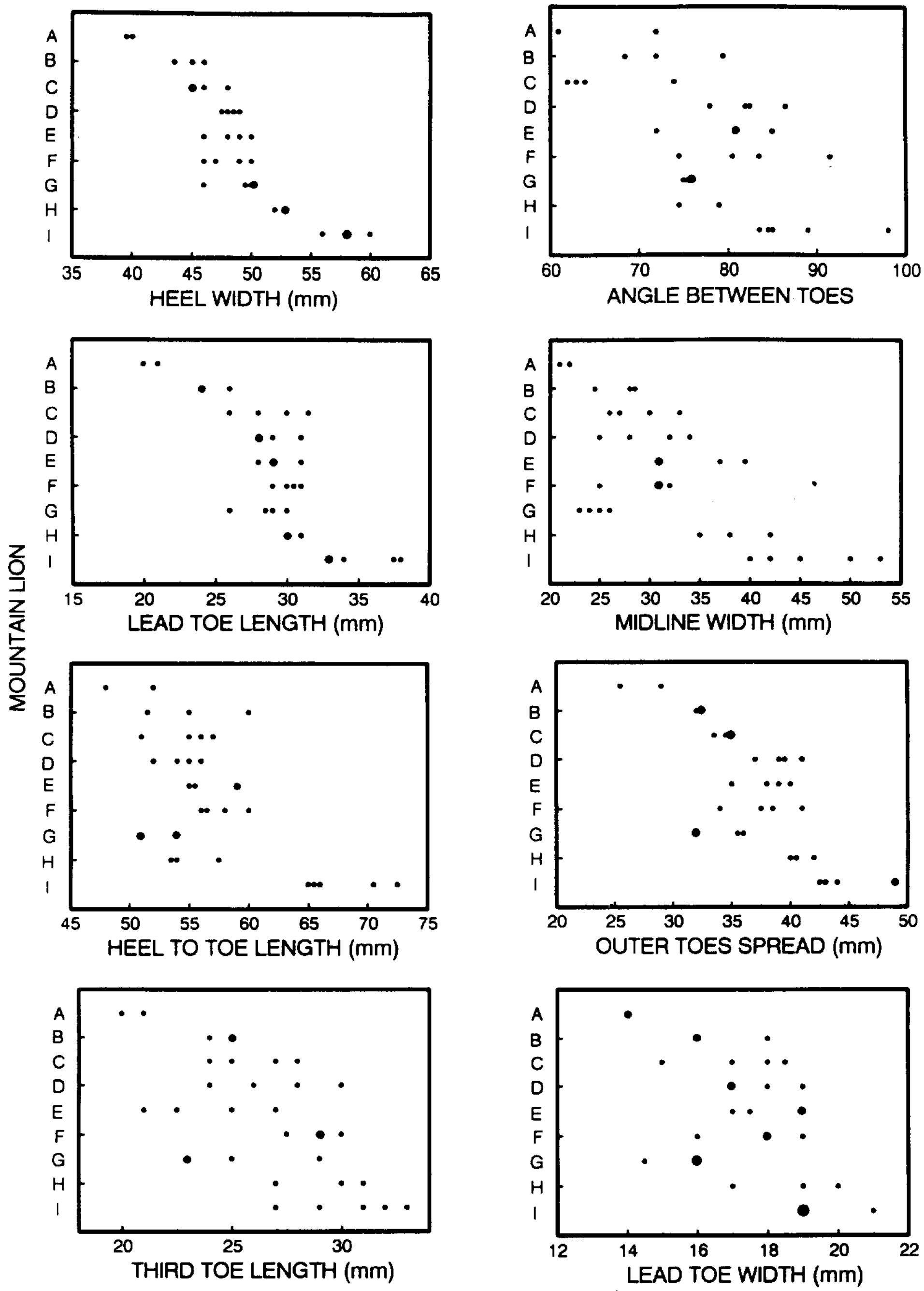

Fig. 3. The measurement values for the left rear tracks of nine mountain lions. Each dot signifies a measurement value, and larger dots signify coincidence of data.

of the right foot differed from that of the left foot.) In the first analysis we used only the first measurement entered stepwise from the most effective model, and in each subsequent analysis we added one more measurement in the order they occurred in that model. Each measurement's contribution was estimated by the: (1) change in effectiveness from one analysis to the next; and (2) summed absolute values of the first two standardized (std) canonical discriminant function coefficients, where the largest summed values correspond with the most effective measurements.

We tested whether effectiveness of the measurements would be consistent among different subsets of mountain lions. We tried 12 analyses per rear foot with different random subsets of 7, 6 and 4 mountain lions. Thus 72 bootstrap analyses were made. The bootstrap technique involves taking new random samples with replacement from the original sample and comparing their misclassifications (Afifi & Clark, 1984, pp. 266–88; Seber, 1984, pp. 289–90). For the subsets of seven and six mountain lions, we tried the eight measurements that contributed to optimal separation of all nine track sets per foot. For the subsets of four track sets, we tried the five measurements with the largest std canonical discriminant function coefficients in the analysis of all nine track sets. We compared the magnitudes of these coefficients in each bootstrap analysis to identify measurements that consistently contributed most to track set separation. We also examined the order consistency of measurements selected stepwise. We expected the measurement selection order to vary among mountain lion subsets.

Table 3. Partition of total error (SE_T) of measurements from tracings of mountain lion rear tracks into observer (measurement and recording) error (SE_0) and error due to slope conditions ($SE_S = SE_T - SE_0$) (in mm)

Measurement	Six different tracks from the same foot			Same tracks from eight different observer postures (angles)			
	Range	$\bar{X}$	SET	Range	$\bar{X}$	SE_0	SE
Middle lobe width[a]	17–18	17·8	0·21	17–21	18·8	0·46	—
Lead toe width	19–23	20·5	0·62	21–22	21·1	0·13	0·49
Third toe length	30–35	32·3	0·73	33–35	33·9	0·24	0·49
Lead toe length	34–39	36·1	0·69	34–36	35·5	0·25	0·44
Heel length	44–49	46·5	0·75	43–45	44·1	0·23	0·52
Outer toes spread	46–54	48·7	1·31	43–46	45·1	0·42	0·89
Midline width	41–53	46·1	0·75	47–50	48·3	0·42	0·33
Heel width	54–60	57·5	0·96	57–58	57·3	0·16	0·80
Heel to lead toe length	63–66	64·3	0·42	62–64	62·9	0·28	0·14
Angle between toes[b]	81–95	86·3	1·89	82–87	83·5	0·61	1·28

[a] Middle lobe width was unique with $SE_0 \geq SE_T$.
[b] Measured in angular degrees.

RESULTS

For the mountain lion track set used to compare errors, the SE (standard error) due to slope averaged 193% of the SE due to recording error among linear measurements, and 210% for the angle between toes (Table 3). The middle lobe width was excluded from the above comparison because its recording error was so large relative to between-track variation that we could not estimate error due to slope. The angle between toes was compared separately from the other measurements because its units were different (this difference presents no problem for its use with discriminant analysis). Slopes most affected the variation of angle between toes, outer toes spread, and heel width, and least affected the variation of heel to lead toe length and middle width (Table 3).

No single measurement adequately discriminated tracks of nine mountain lions (Table 4), because measurement values overlapped extensively (Fig. 3). However, each measurement contributed a unique distribution of values among the mountain lions. With multiple-group discriminant analysis we identified all nine mountain lions by the correct grouping of >75% of the tracks when we used four measurements from the left rear tracks or six measurements from the right rear tracks (Table 5). All left rear tracks and 92% of the right rear tracks were correctly grouped when eight measurements were used. We use Fig. 4 to show the canonical discriminant space for nine mountain lions after eight left rear track measurements were used in multiple-group discriminant analysis to group all their tracks correctly.

Although the order of measurements selected stepwise varied considerably among bootstrap analyses (a condition we expected), their effectiveness was consistent. The 72 bootstraps with four to seven moun-

Table 4. Effectiveness to discriminate nine mountain lions by rear foot tracks when each multiple-group model is a separate measurement ($p < 0{\cdot}0001$ for F-tests of all models)

Measure (analysis)	Percent of tracks correctly grouped[a] to their respective mountain lions for the	
	Left rear foot	Right rear foot
Heel width	51·5	44·4
Midline width	36·4	41·7
Outer toes spread	51·5	41·7
Heel to lead toe length	33·3	38·9
Third toe length	21·2	33·3
Lead toe length	48·5	41·7
Lead toe width	33·3	30·6
Heel length	42·4	30·6
Angle between toes	37·5	—
Middle lobe width	39·4	22·2

[a] Expected effectiveness of 10·9% was based on pure chance, or Σ (prior probability)^2.

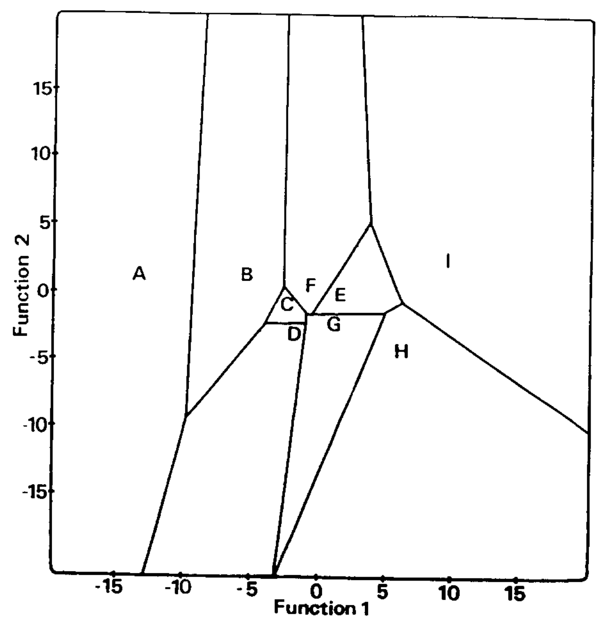

Fig. 4. The discriminant space of all left rear tracks correctly grouped to nine mountain lions with eight track measurements. Each multiple-group discriminant analysis developed two canonical variates; the value of one variate are plotted against those of the other to place tracks in discriminant space. The letters show locations of track set centroids, and corresponds with the letters in Fig. 3.

Table 5. Contributions of measurements (VAR) to the stepwise multiple-group discrimination of nine mountain lions by rear foot tracks
For each foot, eight models were constructed, each with a different number of measurements ($p < 0{\cdot}0001$ for F-tests for all models)

Left rear foot			Right rear foot		
VAR[a]	Percent of 33 tracks correctly grouped	No. of lions identified by >50%, >75% of grouped tracks	VAR[a]	Percent of 35 tracks correctly grouped	No. of lions identified by >50%, >75% of grouped tracks
HW	51·5	5, 4	HW	44·4	4, 2
Add:			Add:		
HLTL	63·6	5, 5	LTL	55·6	4, 3
TTL	75·8	7, 7	MW	72·2	6, 5
LTL	84·9	9, 9	OTS	77·8	7, 6
MW	90·9	9, 9	MLW	83·3	8, 8
ABT	93·8	9, 9	HLTL	88·9	9, 9
OTS	96·9	9, 9	TTL	88·9	9, 9
LTW	100·0	9, 9	ABT	91·7	9, 9

[a] Measurement labels are defined in Fig. 2.

tain lions ranged from 77·8% (one analysis) to 100% (40 analyses) effective, with 27 from 91·7% to 96·7%, and only four from 83% to 87%.

For the most effective model (100%) of all nine left rear track sets, the summed absolute values of the first two std canonical discriminant function coefficients were largest for the distance between the outer toes, heel width, heel to lead toe length, and midline width (Table 6). For the right rear tracks, they were largest for the heel width, spread of the outer toes, midline width, and heel to lead to length (Table 6). The most consistent contributions to track set separation of the 72 bootstrap analyses were from heel width, midline width, and outer toes spread, followed by third toe length, heel to lead toe length, middle lobe width, and lead toe length. All measurements tried in the bootstraps at some point ranked in the top three summed absolute values of the first two std canonical discriminant function coefficients.

DISCUSSION

Although this brief test gave us confidence that we can identify individual mountain lions by their tracks, additional research on recording error and track variability would be helpful. In spite of the high between-track variation for the Georgetown Divide mountain lion, we identified all nine mountain lions by the tracks of either rear foot with multiple-group discriminant analysis. The canonical variates developed in our analysis were very effective with tracks from each rear foot, even though few tracks represented each mountain lion, and the tracks came from an even greater range of slope and substrate conditions than did the Georgetown Divide tracks. We purposely collected tracks from the greatest available range of field conditions so that we could rigorously test the technique. Recording more tracks from each mountain lion under more uniform conditions would enhance their discrimination. If more track sets look similar, as with large samples, discrimination may decrease. Normally the procedure would not be used except for small samples of mountain lions because they are sparsely distributed.

We partitioned the error associated with the Georgetown Divide mountain lion track variation to address the concern that excessive recording error may be associated with the tracing technique and thus limit

Table 6. The contribution of track measurements to model effectiveness

Standardized canonical coefficients for discriminant models of					
Left rear foot (100% effective)			Right rear foot (92%)		
Measure[a]	d.f. 1	d.f. 2.	Measure	d.f. 1	d.f. 2
HW	0·821 5	−0·449 9	HW	0·796 1	0·686 5
OTS	1·091 9	−1·028 9	LTL	0·311 1	0·736 4
HLTL	−0·081 0	1·087 2	MW	−0·140 3	−1·127 3
LTW	0·692 9	−0·132 2	OTS	0·579 8	−0·859 8
LTL	0·269 9	0·286 2	MLW	−0·479 8	0·479 8
ABT	−0·272 9	0·368 7	HLTL	0·668 0	0·066 6
MW	−0·529 7	0·834 6	TTL	−0·107 8	0·745 9
TTL	0·755 4	−0·378 4	ABT	0·342 2	0·240 6

[a] Measurement labels are defined in Fig. 2.

track discrimination (Fitzhugh & Gorenzel, 1985; Fjelline & Mansfield, 1989). However, the between-track variation for this particular mountain lion could have differed from others used in the study, and the recording error for the single track could have been greater than for the other tracks in the study due to Smallwood's use of more postures and angles when tracing it.

Between-track variation was nearly twice as large as recording error for the Georgetown Divide mountain lion. If this is typical of other mountain lions, then either the mountain lion's foot is supple and adjusts its size and shape to different substrate conditions like the tiger *Panthera tigris* (Panwar, 1979), or different substrates cause additional recording error. Nothing can be done to reduce variability from changes in foot shape except to eliminate the most variable measurements (angle between toes, spread of the outer toes, heel width). However, some of these measurements greatly helped discriminate tracks. Recording error may be reduced by using the same angle and posture to record all tracks, and by measuring tracks *in situ*, although the researcher may sometimes damage tracks with the latter technique. Certainly, recording error will increase if tracks are traced by more than one researcher.

We discovered that the total error of the middle lobe width ($SE_T = 0{\cdot}21$, Table 3) was less than the observer error ($SE_0 = 0{\cdot}46$), suggesting that tracing the exact shape of this track feature is more subjective than with other features. Middle lobe width helped discriminate among right but not left rear track sets (Table 5). Although this measurement demonstrated that the discriminating power of within-set variation relative to total variation is robust to recording error, we caution against using such a measurement.

Besides the percentage of cases misclassified (the empirical method), other techniques to measure effectiveness may be used, such as the bootstrap (described in the Methods section) and jackknife (cross-validation) techniques (Seber, 1984, pp. 289–90; Afifi & Clark, 1984, pp. 266–88). The jackknife technique involves withholding a case from the analyses, and then using the derived discriminant functions to classify the omitted case. This can be repeated as many times as there are cases. Certainly, more than one case can be omitted at a time so long as ample size permits. Our sample sizes were too small for the jackknife technique, but samples collected for future track discrimination studies would benefit the researcher if they are large enough to accommodate withholding or randomly choosing track subsets from track sets.

Another technique is to compute the probability of correct classification based on guessing (Afifi & Clark, 1984, pp. 263, 268). The guessing is based on prior probabilities, or the percentage of cases of each group in the sample of tracks. To use the technique, sum the squared prior probabilities for all the groups compared. This value is the percent correct classification to be expected based on pure chance.

Applying the technique to a study site

To help discriminate mountain lion track sets: (1) remove track sets that are different because of *a priori* information (e.g. geographical location, unusual tracks); (2) trace or measure at least four tracks from each track set to improve delineation of measurement distributions; and (3) experiment during analysis by trying different measurements. For analytical reasons there must be more mountain lion tracks compared than measurements used.

Including measurement values from the front tracks when possible may improve discrimination of tracks among mountain lions. We recorded too few front tracks to analyze (11 left front tracks from five individuals, and 10 right front tracks from four individuals). However, those we collected appeared more distinctive among individuals than did rear tracks. Front tracks are not always obtainable because the rear feet often step on the tracks from front feet. If a researcher has enough data from front tracks, we recommend using these in the same way as data from rear tracks.

Stride length and the relative angle of tracks to the line of travel may improve discrimination when track sets are very similar, but these variables may vary greatly with slope conditions and mountain lion behavior. To compare aspects of stride and foot placement, the mountain lions should have walked at normal speeds and on similar terrain.

We do not recommend extrapolating the effectiveness of discriminant functions to tracks made in mud that later dried, or to tracks in deep snow or loose sand. Track size and shape made on these substrates tend to change through time much more than do tracks in fine dust or clay. However, fresh tracks in mud or light snow may be useful when the outline and features of the tracks are distinct and easily measured.

Applying the analysis to new data

A combination of descriptive and predictive discriminant analysis must be used to identify individual mountain lions with multiple track sets from a study site. After optimal group separation is achieved, measurements from the descriptive analysis can be used to predict track set membership of tracks from any newly discovered track sets.

First, arbitrarily assign two track sets to discriminant groups A and B, and analyze these groups by using the track measurements of Fig. 3. However, we stress that the sample size of tracks pooled from two or a few track sets must be at least four times the number of measurements used. If nearly all tracks from each foot are correctly grouped into groups A and B, then these two sets are probably from two mountain lions. If the tracks are about equally mixed between groups, then the two sets are probably from one mountain lion. The criterion to use for a cut-off value for tracks being grouped to individuals or mixed among the same individual is up to the researcher, but should depend heavily on the sample size of tracks. As an initial rule we suggest using 75% correct grouping as cut-off value for small samples (i.e. $n < 6$), and 65% correct grouping for larger samples (i.e. $n \geq 6$).

Pool track sets determined to belong to the same individual into the same group and analyze against a new unidentified track set arbitrarily assigned to the second group. In other words, if groups A and B are determined to belong to the same mountain lion, they should both belong to group A when compared to the next unidentified track set. Or, if A and B are different, for the next analysis you would compare the new unidentified track set as group C. Continue regrouping track sets on a one-to-one basis or cumulatively with multiple-group analyses until all track sets are grouped to individuals. Multiple-group discriminant analysis should provide a base model to identify future track sets discovered on the study site. Thus track set separation and prediction are used interchangeably as a field technique.

When a new track set is entered in an established multiple-group discriminant model the new set will group with the most similar previously identified group(s) whether or not it belongs to that group(s), simply because no discriminant space has yet been allowed for this newcomer. After each newly discovered track set is grouped by this model, apply a two-group discriminant analysis between the new track set and its assigned (most similar) group as described in the previous paragraph. If the new track set does belong to a previously unidentified individual, a new multiple-group discriminant model will be needed. This procedure will quickly become unreliable if the sample sizes for new track sets are not kept large. The prediction that a new track set belongs to a specific individual is more convincing with ten tracks than it is with three.

Measurement choice and research recommendations

Certainly, the track measurements we used (Fig. 3) represent only a small subset of those possible. When other researchers examine tracks carefully, they may identify other worthy traits. We recommend trying as many track measurements as are available in different analyses of the same data set, except those that are highly dependent on others used. Not all measurements initially entered stepwise will necessarily be useful in the discriminant models, because some suppress the effectiveness of others or contribute little (e.g. third toe length in Table 5). Measurements with little discriminating power can destabilize the classification (Williams *et al.*, 1990). From the measurements initially selected stepwise, arbitrarily enter one at a time into new analyses, starting with the measurement originally entered by the computer, and then add the second, and so on (see Table 5). In this way, those measurements contributing little or no effectiveness to the discriminant function(s) can be identified and discarded. Examining the magnitudes of the std canonical discriminant function coefficients can also help identify those measurements that contribute to group separation.

Measurements selected stepwise will differ among data sets because no measurement can possess the same discriminating power relative to that of other measurements among comparisons of different mountain lions (hence the different discriminant models for tracks of each rear foot). However, from our bootstrap analyses we identified some measurements that consistently contributed more to track set separation, and through repeated use of this technique those measurements most often useful should become more apparent. Some measurements may possess large standard errors, but are still effective. The std canonical discriminant function coefficients in Table 6 indicate that the measurements with larger values tend to contribute more to mountain lion discrimination by their tracks.

In other studies (Smallwood & Fitzhugh in press, and unpublished data), we associated mountain lion tracks with roads that had fewer crossroads, and that occurred at lower elevations, along ridges, drainages, and douglas-fir *Pseudotsuga menziesii* and ponderosa pine *Pinus ponderosa* habitats, depending on region. We also found reasonable discrimination of track sets by sex and age classes. With further research, track methods may become more efficient for population study.

With further research our technique also may prove useful for identifying other animals by their tracks, but may be more practical for use with large animals with a fair degree of track complexity (large felids, canids, ursids, cervids, rhinocerotids, etc.). Although recording error did not vary with measurement size ($r = 0{\cdot}32$, $n = 8$, from SE_0 and X_0 of Table 3), a different means of recording small tracks may be required to provide sufficient variation for discrimination. Some form of standardized photography may prove useful. Also, measurements made from plaster casts of tracks may be preferable for certain animals that leave deep tracks in substrates such as mud. For example, Sumatran rhino *Dicerohinus sumatrensis* tracks are deep with considerable shape at the bottom. They cannot be recorded adequately with tracings on acetate overlays but can be recorded with plaster of Paris (van Strien, 1986).

Our method will be useful with cryptic animals for which any information gained is valuable. For example:

(1) Regional population estimates can be improved, especially if the track sets found on an intensive study site are calibrated with demographic and density estimates from another method like radio-telemetry. The results can be extrapolated to other areas by use of track counts.
(2) Capture–recapture analysis can be used without disturbing animals by capture and marking.
(3) Animals visiting multiple scent stations can be detected, and the surveys improved.
(4) Individual movements can be better monitored on a study site.
(5) This method may be helpful in police work when track identification is necessary.

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