



Tools and Technology Article

Traditional Versus Multivariate Methods for Identifying Jaguar, Puma, and Large Canid Tracks

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ABSTRACT The jaguar (*Panthera onca*) and puma (*Puma concolor*) are the largest felids of the American Continent and live in sympatry along most of their distribution. Their tracks are frequently used for research and management purposes, but tracks are difficult to distinguish from each other and can be confused with those of big canids. We used tracks from pumas, jaguars, large dogs, and maned wolves (*Chrysocyon brachyurus*) to evaluate traditional qualitative and quantitative identification methods and to elaborate multivariate methods to differentiate big canids versus big felids and puma versus jaguar tracks ($n = 167$ tracks from 18 zoos). We tested accuracy of qualitative classification through an identification exercise with field-experienced volunteers. Qualitative methods were useful but there was high variability in accuracy of track identification. Most of the traditional quantitative methods showed an elevated percentage of misclassified tracks ($\geq 20\%$). We used stepwise discriminant function analysis to develop 3 discriminant models: 1 for big canid versus big felid track identification and 2 alternative models for jaguar versus puma track differentiation using 1) best discriminant variables, and 2) size-independent variables. These models had high classification performance, with $<10\%$ of error in the validation procedures. We used simpler discriminant models in the elaboration of identification keys to facilitate track classification process. We developed an accurate method for track identification, capable of distinguishing between big felids (puma and jaguar) and large canids (dog and maned wolf) tracks and between jaguar and puma tracks. Application of our method will allow a more reliable use of tracks in puma and jaguar research and it will help managers using tracks as indicators of these felids' presence for conservation or management purposes.

KEY WORDS canids, discriminant function analysis, identification keys, jaguar, *Panthera onca*, puma, *Puma concolor*, track differentiation.

Sign surveys are useful noninvasive tools to assess and monitor elusive or rare species (Wemmer et al. 1996, Gompper et al. 2006). Spoor counts have been used as indicators of presence, relative abundance, and density estimation of different species (Van Dyke et al. 1986, Stander 1998, Crooks 2002, Wilting et al. 2006). Likewise, many studies involving endangered species have used sign surveys to obtain basic ecological information (e.g., distribution and habitat use; Perovic and Herran 1998, Potvin et al. 2005, Markovchick-Nicholls et al. 2008) and as preliminary or complementary assessment in ecological research or conservation plans (Schaller and Crawshaw 1980, Rabinowitz and Nottingha 1986, Soisalo and Cavalcanti 2006, Paviolo et al. 2008). Tracks are not only one of the most commonly used signs but they may also be useful in identifying other associated signs such as fecal samples (Wemmer et al. 1996, Scognamillo et al. 2003, Shaw et al. 2007, Azevedo 2008). However, one of the problems of employing tracks and other signs is correct identification of the species, particularly in areas where ≥ 2 similar species are likely to be found and where little or no information about their presence is available.

Because track shape is affected by many factors (like substrate quality or the pace of the animal) it is often difficult to distinguish tracks of similar species, particularly in areas where soil conditions make track printing difficult

and only few tracks are found in each event (Fjelline and Mansfield 1988, Wemmer et al. 1996, Grigione et al. 1999, Lewison et al. 2001). Multivariate analyses have been used to reduce subjectivity and improve accuracy in sign recognition (Zielinski and Truex 1995, Zalewski 1999, Harrington et al. 2008, Steinmetz and Garshelis 2008). In addition, multivariate analyses of feline tracks have been used for more demanding objectives like sex determination and individual identification (Smallwood and Fitzhugh 1993, Riordan 1998, Sharma et al. 2003, Wilting et al. 2006, Isasi-Catalá and Barreto 2008; but see Karanth et al. 2003 and Gordon et al. 2007).

Jaguars (*Panthera onca*) live in sympatry with pumas (*Puma concolor*) along most of their distribution and both species are the focus of many research and conservation programs (Nowell and Jackson 1996, Sanderson et al. 2002, Conroy et al. 2006, Shaw et al. 2007). These felids also share most of their range with some large canids, such as pumas with gray wolves (*Canis lupus*) and coyotes (*C. latrans*) in North America, both felids with the maned wolf (*Chrysocyon brachyurus*) in central South America, and both felids with the domestic dog in most of their distribution.

Tracks of pumas and jaguars have been employed for research, monitoring, and management (Smallwood and Fitzhugh 1995, Hoogesteijn 2007, Shaw et al. 2007). However, it is often difficult to differentiate between puma and jaguar tracks because they are similar in size and shape and both are frequently confused with big canids' tracks

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(Smallwood and Fitzhugh 1989, Childs 1998, Shaw et al. 2007). For this reason, many authors have described qualitative traits to differentiate puma from dog tracks (Smallwood and Fitzhugh 1989, Shaw et al. 2007; Appendix A), and to distinguish jaguar from puma tracks (Schaller and Crawshaw 1980, Aranda 1994, Childs 1998; Appendix A). Nevertheless, due to the subjectivity and exceptions found in application of qualitative traits, some authors proposed quantitative identification measures (Belden 1978, Smallwood and Fitzhugh 1989, Aranda 1994, Childs 1998, Shaw et al. 2007; Appendix B). However, these quantitative criteria were created and evaluated based on either few known individuals or unknown field tracks classified by qualitative traits.

In view of these shortcomings, we used a diverse set of tracks from definitely known origin with the aim of 1) evaluating performance of qualitative and quantitative methodologies described to differentiate tracks of big canids, pumas, and jaguars; and 2) developing accurate and robust quantitative multivariate criteria to classify tracks of these groups and species.

STUDY AREA

Between 2004 and 2008, we obtained track records from jaguars, pumas, and maned wolves kept in captivity. Our task was carried out in collaboration with 18 zoos from 6 countries: Zoo Batán (Batán, Argentina), Zoologico Bosque Guarani (Foz do Iguacu, Brazil), Refugio Biologico Bela Vista (Foz do Iguacu, Brazil), Zoológico Itaipú Paraguay (Hernandarias, Paraguay), Parque Ecológico Urbano de Río Cuarto (Río Cuarto, Argentina), Zoológico de la Ciudad de Buenos Aires (Buenos Aires, Argentina), Temaikén (Buenos Aires, Argentina), Zoológico de Roque Sáenz Peña (Roque Sáenz Peña, Argentina), Zoológico Tatú Carreta (La Cumbre, Argentina), Jardín Zoológico de la Ciudad de Córdoba (Córdoba, Argentina), Zoológico Santa Fe de Medellín (Medellín, Colombia), Parque Zoológico Caricuao (Caracas, Venezuela), Parque Zoológico Las Delicias (Maracay, Venezuela), Lincoln Park Zoo (Chicago, IL, USA), Sedgwick County Zoo (Wichita, KS, USA), Caldwell Zoo (Tyler, TX, USA), Philadelphia Zoo (Philadelphia, PA, USA), and Little Rock Zoo (Little Rock, AR, USA).

METHODS

Sample Collection and Processing

We collected tracks from 28 jaguars, 29 pumas, and 8 maned wolves (mainly ad of both sexes for all the species, although we also included 2 tracks of a juv jaguar and 3 tracks of 2 juv pumas of around 1.5 yr old). We used the same methodology to obtain large dog tracks from urban areas (35 individuals, most of them stray dogs). Authors and zoo personnel recorded tracks by following general recommendations (see Wemmer et al. 1996, De Angelo et al. 2008) instead of standardized methodology, because our main objective was to evaluate identification methods for tracks collected in the field by different people, under diverse circumstances, and using different protocols. For the same reason, we used tracks

for as many individuals and zoos as possible, looking for all kind of tracks (front, rear, right, and left feet), diverse substrates, and different animal size and behavior (to favor including track variability caused by animal pace and wt). We collected all tracks from free-walking animals (i.e., the paw was not pressed into the substrate by handlers). We obtained all dog tracks and 78% of tracks from zoos from unprepared substrates, whereas remaining zoo tracks were from sleekly prepared surfaces on which animals walked freely to yield better prints (mainly in zoos lacking an adequate surface for printing tracks). Substrate conditions varied among zoos and among the sites where we collected dog tracks, including mud, dust, and sand (wet or dry), for all groups considered. We tried to collect as many tracks as possible from each individual. However, because we obtained few tracks in most of the zoos, we tried to select ≤ 1 track/foot from each individual, in order to have all individuals represented by the same number of tracks. We used 3 methods for recording tracks: plaster molds, digital photos with a metric rule as size reference, and track contour in acetate paper. Multiplicity of zoos, individuals, collectors, and methods generated a variety of tracks of different qualities, from which we only discarded for further analysis those tracks that had conspicuous deformations precluding an accurate measurement.

To give digital format to collected data, we photographed the plaster molds with digital cameras and scanned track tracings, including a metric rule. Then, the first author digitalized all tracks using the spline tool in AutoCAD® 2004 (AutoDesk, Inc., Fresno, CA). For digitalization and measurement, we scaled tracks according to the size-reference metric rule. Subsequently, we rotated and placed tracks over a base line defined by a tangent line between the outer heel lobes (Smallwood and Fitzhugh 1989; Fig. 1).

We analyzed 167 tracks, including plaster molds ($n = 98$), photographs ($n = 57$), and track tracings ($n = 12$) from the 3 groups of interest. We randomly separated 35 tracks out of the total (10 jaguars, 10 pumas, and 15 big canids) to be used only for independent validation for discriminant models and identification keys (independent cases). We used all other 132 tracks in traditional method validation and for multivariate model and identification key development (46 tracks from jaguars, 46 from pumas, 33 from dogs, and 7 from maned wolves).

Evaluation of Traditional Identification Methods

To evaluate accuracy of traditional qualitative track identification we made a classification exercise with 67 participants from Argentina, Brazil, and Paraguay in a jaguar conservation meeting (Third Workshop of Collaborative Effort for Jaguar Monitoring in Atlantic Forest, 5–6 Oct 2005, Puerto Iguazú, Misiones, Argentina). Although participants considered themselves capable of identifying tracks of these carnivores (jaguars, pumas, and big canids), we started the exercise by showing examples of tracks from each group and by reviewing traditional qualitative differentiation characters (Appendix A). From our track database, we randomly selected 10 photographs of tracks from each group and then asked volunteers to classify tracks into these

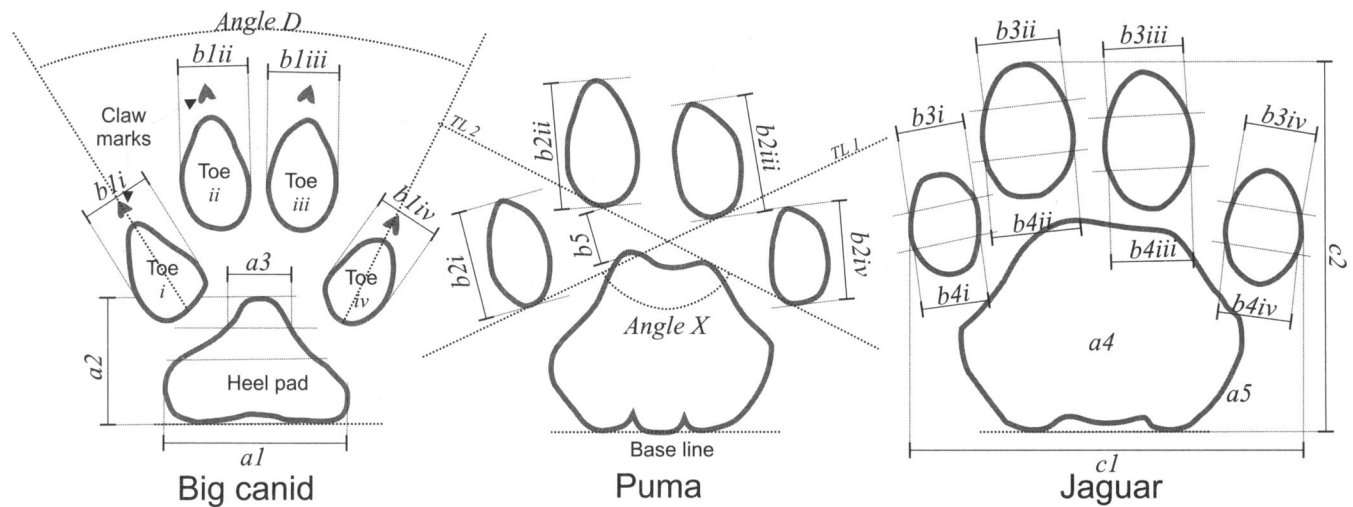


Figure 1. Examples of typical big canid, puma, and jaguar tracks. We used measurements shown in this figure for the validation of quantitative identification criteria and for construction of variables used in discriminant analysis to develop a multivariate identification method for tracks of these species. We collected samples from 18 zoos from Argentina, Brazil, Colombia, Paraguay, United States, and Venezuela, and urban areas from Argentina, 2004–2008. (a) Heel pad: $a1$: total width, $a2$: total length, $a3$: width at the third quarter of the total length ($a2$ needed), $a4$: total area, $a5$: total perimeter. (b) Toes: $b1$ (i to iv): total width, $b2$ (i to iv): total length, $b3$ (i to iv): width at the first third of the total length ($b2i$ – $b2iv$ needed), $b4$ (i to iv): width at the second third of the total length ($b2i$ – $b2iv$ needed), $b5$: the higher distance between toes and the heel pad. (c) Track: $c1$: total width, $c2$: total length. $TL1$: tangent line created between the base of toes i and iii , $TL2$: tangent line created between the base of toes ii and iv , $Angle D$: angle between the longitudinal axes of i and iv toes, $Angle X$: inferior angle formed between $TL1$ and $TL2$ lines.

3 categories during a slide presentation of photographs of the tracks. Finally, we marked the achievement of each volunteer by the percentage of correctly classified tracks, and contrasted their performance with 67 randomly simulated classifications.

We selected 4 categorical variables proposed for differentiation of big canids from felids (i.e., claw marks, shape of heel-pad front area, shape of heel-pad base, and shape of the inner side of outer toes; Appendix A), and we assessed percentage of correctly classified tracks by each feature. We used 33 dog, 46 puma, and 46 jaguar tracks to validate existent quantitative classification criteria (Appendix B). We also included 7 maned wolf tracks to assess whether they were classified in the same group as dog tracks. For each criterion, we observed the number of correctly and misclassified tracks. Following the statement by Aranda (1994) that any of the toes could be used in his criterion, we used all toes in each track to test it.

Construction and Validation of Multivariate Models

We created a series of measurements and combinations of measurements for representing quantitatively each of the described qualitative traits for track differentiation (Appendix A). We also incorporated existing quantitative criteria (Appendix B) as they were originally described and with some modifications (e.g., see VarA2 and VarB3 in Appendix C). This procedure resulted in 155 measurements and variables that included linear, angular, and area dimensions, proportional variables composed by ratios among ≥ 2 measurements, and shape variables as described by Lewison et al. (2001). To reduce the total number of variables, we randomly selected 20 tracks from each group (jaguars, pumas, and big canids) and assessed variable performance in track differentiation using box-plot graphs and indepen-

dent-sample t -tests. We maintained as preselected variables only those that showed significant differences between groups in univariate tests. We also checked these variables for redundancy by using Pearson correlations. From groups of highly correlated variables ($r > 0.8$), we selected only the variable that showed the largest univariate difference between groups (the highest t value). When ≥ 2 correlated variables showed similar univariate differentiation capability, we selected the variable that featured more simplicity for precise measurement (Zielinski and Truex 1995).

We combined preselected variables and a set of tracks from each group (original training cases) in discriminant function analysis (DFA). We created models to differentiate 1) big canid tracks from those of big felids, and 2) puma tracks from those of jaguars. To construct each model, we conducted stepwise variable selection using Wilks' lambda criterion, choosing the minimum number of less correlated variables but ensuring the highest group differentiation (min. partial F to enter = 3.84; max. partial F to remove = 2.71; SPSS 2008, Steinmetz and Garshelis 2008). We validated models by percentage of original training cases correctly classified, percentage of cross-validated cases correctly classified (leave-one-out classification), and percentage of independent cases (tracks not used for model development) correctly classified (SPSS 2008, Steinmetz and Garshelis 2008). Additionally, we evaluated model performance by estimating probabilities of group membership for all cases, both for misclassified and correctly classified training and independent tracks (see Stockburger 1998).

Jaguars are bigger than pumas and body size is correlated with track size (Crawshaw 1995, Sunquist and Sunquist 2002); therefore, absolute size proves to be useful in track differentiation (Childs 1998, Brown and Lopez Gonzalez 2001). However, both species show high variation in size along their

distribution and their size ranges overlap extensively (Iriarte et al. 1990, Sunquist and Sunquist 2002). Most of our jaguar tracks were bigger than puma tracks (pad width for pumas: \bar{x} = 5.06 cm, SD = 0.79, n = 46; and for jaguars: \bar{x} = 7.14 cm, SD = 1.05, n = 46). Inclusion of all tracks in model training caused classification errors only with the biggest puma and smallest jaguar tracks due to an overrated importance of size in track classification. These intermediate size tracks are commonly the most difficult tracks to identify, even for experts. Accordingly, we selected the 50th percentile containing smaller jaguar tracks and the 50th percentile containing bigger puma tracks as model-training tracks for puma versus jaguar discriminant models to reduce the relative importance of size-related variables. In addition, we produced a model with all tracks without including absolute measurements related with track size.

From the final variables used in discriminant models, we selected easier-to-measure variables to make simpler discriminant models. We used these simpler models as steps to construct track identification keys (Steinmetz and Garshelis 2008). We determined the ranges for step decisions by the function discriminant scores (DS) that represented 90–99% of posterior probabilities of group membership (Stockburger 1998). We started each key with the easiest-to-measure variables and the simplest model, and then we used more complex models in each step (adding more variables), to make the identification process easy to perform.

We took all measurements using Auto Cad to the nearest 0.01 cm for linear measurements, 0.01 cm² for areas, and 1° for angles. We assessed normality and homoscedasticity of variables with the Shapiro–Wilk and Levene’s test and applied reciprocal, natural logarithm, square, or cubic transformation when needed. We used the Box’s M statistic to test for the homogeneity of covariance matrices. We conducted all statistical analyses using SPSS® for Windows statistical package version Rel.11.0.1.2001 (LEAD Technologies, Inc., Chicago, IL).

RESULTS

Reliability of Previously Described Identification Methods

Volunteers correctly classified $61.5 \pm 1.4\%$ ($\bar{x} \pm$ SE) of tracks, a larger percentage than that obtained by a random classification (\bar{x} = 35.1%, SE = 1.0%, n = 67; Mann–Whitney test: Z = -9.45, P ≤ 0.001). However, nobody correctly classified all tracks, and participants showed a wide range of identification accuracy (37–87%) with higher variation than that observed in random classification (volunteers classification SD = 11.2%, random classification SD = 8.1%; $F_{66,66}$ = 1.9, P < 0.02; Sokal and Rohlf 1995). Although 67% of tracks were correctly identified by >50% of volunteers, a group of 10 hard-to-identify tracks (including canid, puma, and jaguar tracks) were incorrectly identified by >50% of volunteers.

Criterion described by Belden (1978; Appendix B) showed >20% of dog and puma tracks misclassified but had better performance identifying maned wolf tracks as canids and jaguar tracks as felids (Table 1). Criterion described by

Table 1. Classification accuracy of traditional quantitative methods described to differentiate big canids versus big felids tracks (mainly described for dog vs. puma tracks) and puma versus jaguar tracks. We made our evaluation using tracks from 18 zoos of Argentina, Brazil, Colombia, Paraguay, United States, and Venezuela, and urban areas from Argentina, 2004–2008 (dog n = 33, maned wolf n = 7, puma n = 46, jaguar n = 46). See description of criteria in Appendix B.

Criterion	% of misclassified tracks			
	Dog	Maned wolf	Puma	Jaguar
Belden (1978) ^a	45	0	24	4
Smallwood and Fitzhugh (1989) ^a	21	14	17	9
Shaw et al. (2007) ^b			0	0
Aranda (1994) ^{c,d}			87	0
Childs (1998) ^{a,e}			15	18

^a Criterion described to differentiate dog vs. puma tracks.

^b Criterion described only to characterize puma tracks.

^c Criterion described to distinguish puma vs. jaguar tracks.

^d Criterion evaluated independently for each toe print of the tracks.

^e Criterion described for rear tracks and evaluated only with 17 jaguar and 13 puma tracks, because many of the collected tracks did not have accurate information in this aspect.

Smallwood and Fitzhugh (1989) presented better reliability in dog and puma track differentiation, but showed a higher error with maned wolf and jaguar tracks than the method described by Belden (1978; Table 1). All puma and jaguar tracks had >3.5 cm of heel-pad width as described by Shaw et al. (2007) for puma (Table 1). To differentiate puma and jaguar tracks, criterion by Aranda (1994; Appendix B) showed the highest error, misclassifying >80% of puma toes, although all jaguar toes were correctly identified (Table 1). The ratio of pad area to track area of rear tracks described by Childs (1998) had better classification accuracy (Table 1), but we evaluated accuracy for 17 jaguar and 13 puma tracks only, and 23% of evaluated tracks fell into the undefined intermediate range. Considering the total heel-pad width (Appendix B), ranges between rear tracks of puma and jaguar from zoos overlapped (puma range = 4.07–5.50 cm; jaguar range = 5.18–8.99 cm) with one puma and one jaguar rear track in the overlapping range (Childs 1998, Brown and Lopez Gonzalez 2001; Appendix B).

Two categorical features showed the expected pattern with >70% of puma and dog tracks correctly classified, but the other 2 categorical variables misclassified >60% of dog tracks (Fig. 2). Claw marks were absent in 93.5% of puma tracks whereas 97% of dog tracks presented claw marks (Fig. 2A). The front of the heel pad was flatter or concave in 84.8% of puma tracks and 72.7% of dog tracks presented rounded or pointed shape in the front of the heel pad. Jaguar and puma tracks showed similar classification percentages using these variables, as did maned wolf and dog tracks (Fig. 2A, B), but no variable allowed differentiation of 100% of tracks among these species. Contrary to what was expected, 63.6% of dog tracks showed a tri-lobbed heel-pad base and 72.7% presented a rounded inner part of the outer toes (Fig. 2C, D). In addition, it was sometimes difficult to classify, unambiguously, tracks into the categories defined by these last 2 categorical variables (i.e., shape of the base of the heel pad and inner shape of the outer toes).

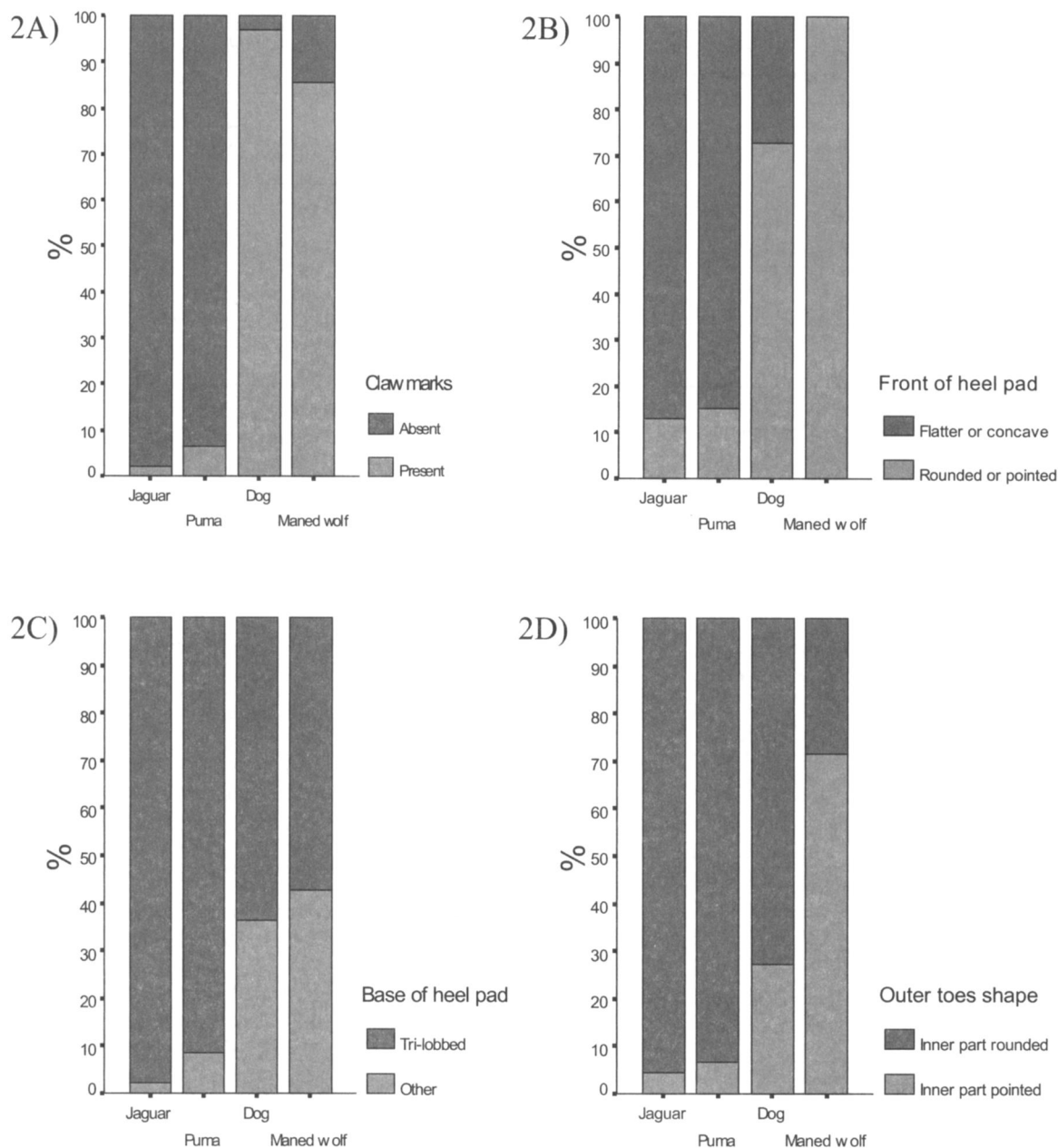


Figure 2. Percentage of tracks bearing different characteristics related with 4 categorical variables used for canid and felid track differentiation. A) Presence or absence of claw marks; B) shape of the front of the heel pad; C) shape of the base of the heel pad; D) shape of the inner part of the outer toes. We evaluated tracks from pumas ($n = 46$), jaguars ($n = 46$), dogs ($n = 33$), and maned wolves ($n = 7$) that we collected from 18 zoos from Argentina, Brazil, Colombia, Paraguay, United States, and Venezuela, and urban areas from Argentina, 2004–2008. See a complete description of these characteristics in Appendix A.

Multivariate Model Construction and Validation

We preselected 35 variables that showed more differentiation capability between the groups we analyzed. Stepwise DFA starting with these variables resulted in 3 discriminant models (Table 2; Fig. 3) constructed by different combinations of 10 of these preselected variables (see Appendix C).

For big canid versus big felid track contrast, we selected a model composed by 3 variables that proved to be >98% accurate in all validation procedures (model A1; Table 2; Fig. 3A). Classification errors of this model occurred with one puma and one jaguar track that were classified as canid, with group probabilities of 69% and 88%, respectively (Table 3). However, 82% of training and 83% of independent tracks from felids and canids were correctly classified

with high membership probabilities (>95%; Table 3), with pumas having lower probabilities than jaguars within the felid group (Fig. 3A).

To differentiate puma and jaguar tracks, we selected 2 models (models B1, B2; Table 2; Fig. 3B, C). We generated model B1 from a stepwise process starting with all preselected variables, and model B2 only used size-independent variables. Model B1 included transformed pad width (VarB1) as a size parameter, so we developed this model using only bigger puma tracks ($\bar{x} = 5.67$ cm, SD = 0.65 cm, range = 4.99–7.46 cm, $n = 23$) and smaller jaguar tracks ($\bar{x} = 6.35$ cm, SD = 0.53 cm, range = 4.99–7.02, $n = 23$), whereas we used excluded tracks only for model validation. Model B1 had higher group separation

Table 2. Parameters, variables incorporated, discriminant functions, and validation results for discriminant models selected for felid versus canid (A1) and for puma versus jaguar track differentiation (B1 and B2). To develop these models we collected samples from 18 zoos from Argentina, Brazil, Colombia, Paraguay, United States, and Venezuela, and urban areas from Argentina, 2004–2008.

Groups	Model	Wilks' lambda (λ) and associated χ^2	Discriminant function ^a	Validation		
				Original cases	Cross-validation	Independent cases ^b
Felids vs. canids	A1	$\lambda = 0.280$ $\chi^2_3 = 163.1^*$	$DS = 10.711 \times \text{VarA1} + 1.563 \times \text{VarA3} + 0.047$ $\times \text{Angle X} - 16.126$	98.5%	98.5%	100.0%
Jaguars vs. pumas	B1	$\lambda = 0.206$ $\chi^2_4 = 63.97^*$	$DS = 5.412 \times \text{VarB1} + 2.806 \times \text{VarB2} + 10.865$ $\times \text{VarB4} + 0.342 \times \text{VarB5} - 8.936 \times \text{VarB7}$ $- 0.261 \times \text{VarB8} - 0.942 \times \text{VarB9} - 15.765$	100%	93.5%	100.0%
	B2	$\lambda = 0.282$ $\chi^2_4 = 110.19^*$	$DS = 4.052 \times \text{VarB2} + 7.710 \times \text{VarB4} + 0.207$ $\times \text{VarB5} - 3.525 \times \text{VarB7} - 0.072 \times \text{VarB8}$ $- 1.672 \times \text{VarB9} - 7.659$	96.7%	94.6%	95.0%

^a Function used to calculate the discriminant score (DS) to classify tracks. See Appendix C for variable descriptions.

^b Independent validation in model B1 consists of independent cases plus excluded cases.

* $P < 0.001$.

(i.e., lower Wilks' lambda) and higher values in the 3 validation methods than model B2 (Table 2). No original, excluded, or independent tracks were misclassified and 90% of tracks were classified with >95% of membership probabilities (Table 3; Fig. 3B). Model B1 incorporated 7 variables that needed 19 measurements (Table 2).

Model B2 incorporated 6 size-independent variables (19 measurements needed; Table 2). Although model B2 had lower performance than model B1 (Table 2), it misclassified only 1 jaguar and 3 puma tracks, but with medium to high group probabilities (58–95%; Table 3; Fig. 3C).

We constructed 3 identification keys: one for the contrast between canids and felids and 2 for identifying puma from jaguar tracks (with and without size-related variables, respectively).

Key 1.—Big canid versus big felid track identification.

Step A: Calculate VarA1 (see Appendix C)

A1. <0.41 : canid.

A2. >0.67 : felid.

A3. 0.41 – 0.67 : go to step B.

Step B: Calculate discriminant score using:

$$DS = 12.532 \times \text{VarA1} + 1.962 \times \text{VarA3} - 12.458$$

B1. $DS < -1.60$: canid.

B2. $DS > 0.01$: felid.

B3. $DS = -1.60$ – 0.01 : use discriminant model A1.

This key used 2 variables incorporated in 2 steps (6 measurements needed to complete the key). This key failed to classify 19% of training tracks and 20% of independent tracks, which then required use of discriminant model A1 to attain a final classification.

Key 2.—Puma versus jaguar track identification using track size.

Step A: Measure the heel-pad width (measurement a1)

A1. <4.5 cm: puma.

A2. >7.9 cm: jaguar.

A3. 4.5 – 7.9 cm: go to step B.

Step B: Calculate discriminant score using:

$$DS = 6.528 \times \text{VarB1} + 0.077 \times \text{VarB8} - 14.627$$

B1. $DS < -2.40$: puma.

B2. $DS > 1.95$: jaguar.

B3. $DS = -2.40$ – 1.93 : go to step C.

Step C: Calculate discriminant score using:

$$DS = 5.890 \times \text{VarB1} - 8.088 \times \text{VarB7} + 0.024$$

$$\times \text{VarB8} - 9.830$$

C1. $DS < -1.90$: puma.

C2. $DS > 1.80$: jaguar.

C3. $DS = -1.90$ – 1.80 : go to step D.

Step D: Calculate discriminant score using:

$$DS = 6.539 \times \text{VarB1} + 10.222 \times \text{VarB4} - 10.762$$

$$\times \text{VarB7} - 0.039 \times \text{VarB8} - 6.029$$

D1. $DS < -1.00$: puma.

D2. $DS > 1.55$: jaguar.

D3. $DS = -1.00$ – 1.55 : use discriminant model B1.

This key used total heel-pad width in the first step but because it was a one-variable-size-related step, we selected an extreme range (the chosen values represent >99% of membership probabilities in one-variable discriminant model). The key required 4 variables (13 measurements), and 41% of training, 4% of excluded, and 25% of independent tracks remained unidentified and required the use of discriminant model B1 for further discrimination.

Key 3.—Puma versus jaguar track identification without using track size.

Step A: Calculate heel pad:track area ratio (VarB8; Childs 1998)

A1. $<24.5\%$: puma.

A2. $>50\%$: jaguar.

A3. 24.5 – 50% : go to step B.

Step B: Calculate discriminant score using:

$$DS = 3.989 \times \text{VarB7} - 0.094 \times \text{VarB8} + 3.156$$

$$\times \text{VarB9} - 2.142$$

B1. $DS > 1.75$: puma.

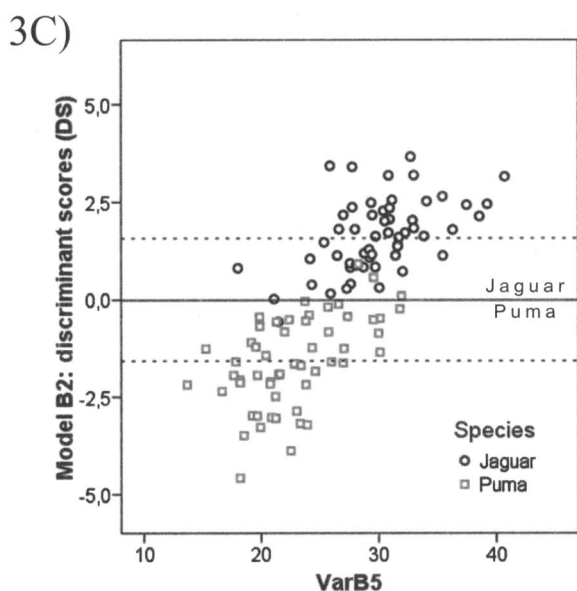
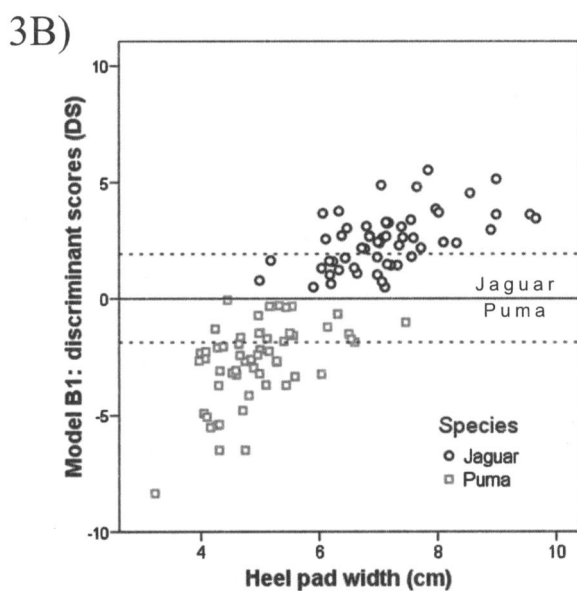
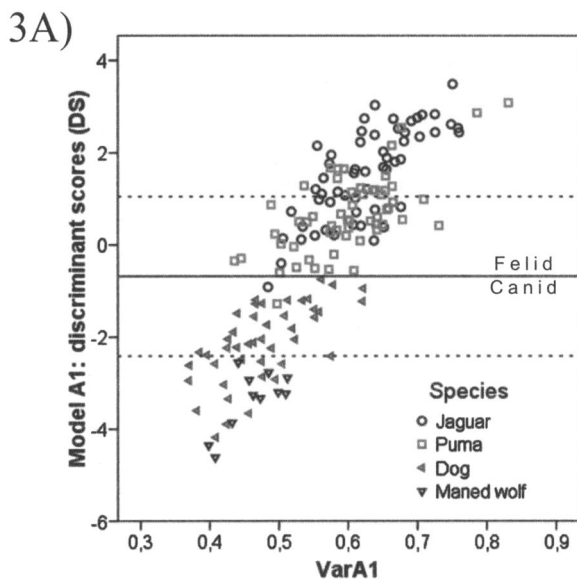


Figure 3. Distribution of tracks along the variable with the highest differentiation ability between groups (horizontal axis), against distribution

- B2. $DS < -2.26$: jaguar.
 B3. $DS = -2.26-1.75$: go to step C.

Step C: Calculate discriminant score using:

$$DS = 7.885 \times \text{VarB4} - 4.043 \times \text{VarB7} + 0.077 \times \text{VarB8} - 2.487 \times \text{VarB9} - 4.477$$

- C1. $DS < -1.40$: puma.
 C2. $DS > 1.50$: jaguar.
 C3. $DS = -1.40-1.50$: use discriminant model B2.

The key required 4 size-independent variables (17 measurements), and 53% of training and 55% of independent tracks remained unidentified and required the use of discriminant model B2 for further discrimination.

DISCUSSION

Described Methods for Jaguar and Puma Track Identification

Although not a real field-track recognition situation, the identification exercise showed that qualitative traits are useful for track distinction. At the same time, it also revealed ambiguity and subjectivity in criteria application resulting in high variation in classification accuracy. All participants were trained together in track recognition before the exercise; however, variation in the performance among volunteers was higher than that observed in random classifications. Although volunteers (mainly biologists and park rangers) had experience in fieldwork, not all of them had the same expertise in track recognition. Previous experience in identifying tracks is probably the main reason for this variability in participants' classification rate. Several authors have mentioned the relevance of field expertise in sign identification (Wemmer et al. 1996, Stander et al. 1997, Childs 1998, Shaw et al. 2007), but the frequent assumption that people with field experience possess sign recognition skills does not always hold true (Lynam 2002).

Existing quantitative univariate criteria showed low accuracy in track classification. The technique by Belden (1978) had a high misclassification rate ($>20\%$) and criterion by Smallwood and Fitzhugh (1989), though more accurate, also misclassified nearly 20% of puma and dog tracks. Likewise, for jaguar and puma track recognition we obtained low classification rates with criterion by Aranda

←

of tracks along discriminant models (vertical axis) obtained to differentiate A) canid versus felid tracks, B) puma versus jaguar tracks using size-dependent variables, and C) puma versus jaguar tracks using size-independent variables. We included both training and independent tracks in the graphs (jaguar $n = 56$; puma $n = 56$; dog $n = 44$; maned wolf $n = 11$). Horizontal continuous line indicates the limit among groups predicted by the model, and horizontal dashed lines indicate the centroid value for each group. VarA1: width at the third quarter of the heel pad, divided by the total heel-pad width. VarB5: actual area of the heel pad divided by the squared area of the track (total track width \times total track length) expressed as percentage. We collected samples from 18 zoos from Argentina, Brazil, Colombia, Paraguay, United States, and Venezuela, and urban areas from Argentina, 2004–2008.

Table 3. Discriminant score ranges and their approximately associated probability for each discriminant model that we developed to differentiate tracks of canids, pumas, and jaguars. Number of misclassified and well-classified training and independent tracks are shown for each range. To develop these models, we collected samples from 18 zoos from Argentina, Brazil, Colombia, Paraguay, United States, and Venezuela, and urban areas from Argentina, 2004–2008.

Model	Groups	Centroid value	Discriminant score	Group probability ^a	Misclassified tracks			Well-classified tracks		
					Training	Excluded	Independent	Training	Excluded	Independent
A1	Canids	-2.411	<-2.000	>99% canid	0		0	26		10
			-2.000 to -1.086	80–99% canid	1		0	13		3
			-1.085 to -0.739	55–79% canid	1		0	1		2
	Felids	1.048	-0.738 to -0.623	Undetermined ^b	0		0	0		0
			-0.624 to -0.277	55–79% felid	0		0	8		1
			-0.278 to 0.650	80–99% felid	0		0	26		6
		>0.650	>99% felid	0		0	56		13	
B1	Pumas	-1.920	<-1.2	>99% puma	0	0	0	18	22	8
			-0.769 to -0.361	80–99% puma	0	0	0	3	0	1
			-0.360 to -0.052	55–79% puma	0	0	0	2	1	1
	Jaguars	1.92	-0.051 to 0.051	Undetermined ^b	0	0	0	0	0	0
			0.052 to 0.360	55–79% jaguar	0	0	0	0	0	0
			0.361 to 0.769	80–99% jaguar	0	0	0	6	2	0
		>1.2	>99% jaguar	0	0	0	17	21	10	
B2	Pumas	-1.579	<-1.450	>99% puma	0		0	26		4
			-1.450 to -0.439	80–99% puma	1		0	14		3
			-0.438 to -0.064	55–79% puma	0		0	3		2
	Jaguars	1.579	-0.063 to 0.063	Undetermined ^b	1		0	1		0
			0.064 to 0.438	55–79% jaguar	0		1	4		1
			0.439 to 1.450	80–99% jaguar	2		0	15		3
		>1.450	>99% jaguar	0		0	25		6	

^a Ranges of approx. group membership probabilities estimated using a posteriori probabilities calculated by SPSS for all cases (Stockburger 1998, SPSS 2008).

^b Although 50% probability determines the limit between 2 groups, we considered that the difference in values around 50% is too scarce to be used as criterion for unknown track classification.

(1994), which misclassified most puma track toes. Heel pad:track area ratio showed better results for distinguishing rear tracks, but we only evaluated a few tracks and it is not always possible to determine rear and front tracks under field conditions. Heel-pad width of rear tracks presents the same limitation and depends on regional size variation of these species. Well-defined ranges in a specific region could probably render this criterion locally useful for preliminary track identification in the field.

Only 2 categorical variables were suitable for discriminating big canid from big felid tracks. Nevertheless, none of these variables demonstrated a 100% classification rate and sometimes tracks could not be included with certainty in the categories defined by these variables. Subjectivity in variable assessment could introduce important biases in track classification. Smallwood and Fitzhugh (1989) found similar results in their exploratory evaluation, and we agree with the assessment by those authors that presence and absence of claw marks and the front of the heel pad were the most useful categorical variables.

A likely explanation for misclassifications using previously described quantitative and categorical techniques is that we selected a set of tracks with different qualities from different individuals, zoos, and substrates, instead of using only high-quality tracks collected in standardized and controlled conditions. Most of these methods were originally tested with only a few known tracks from zoos or mostly with tracks collected in the field (see Appendix B), and this practice could not only present the problem of possible misidentification of the field track, but also introduce a bias

toward including only well-defined tracks (easiest to identify in the field; Lynam 2002, Sharma et al. 2003). However, when using zoo tracks (or tracks from dogs in urban areas) instead of field tracks, we are possibly introducing a bias related to differences between natural substrates and zoo substrates. Additionally, we would expect differences in paw characteristics and pace of animals walking inside zoo cages or dogs in urban areas versus animals walking freely in field areas. Geographic variation in animals and soil condition may also influence the misclassification rate of these methods. All of these methods were originally developed in a restricted region (i.e., criteria by Belden and by Smallwood and Fitzhugh in part of the United States, criteria by Aranda in part of Mexico, and criteria by Childs in the Brazilian Pantanal; Appendix B), though we evaluated these methods with tracks from animals of many zoos from 6 countries. Nevertheless, and despite the low accuracy, all of these quantitative traits were preselected as variables for the multivariate analysis and many of them were used in final discriminant models (Appendix C).

Multivariate Track Classification Method

All discriminant models had statistically significant group differentiation capabilities, and independent track classification had $\geq 95\%$ discrimination accuracy in all models. As mentioned above, the set of tracks used for construction and validation of models included high variability because it incorporated tracks from males and females, from rear, front, right and left foot, as well as tracks from many substrates and of various qualities. Thus, the high discriminant rates we achieved with our models suggest

that they are robust, and they could be used to classify unknown tracks in field studies.

However, all models had ≥ 1 misclassified track in cross-validation classification, and occasionally in original cases reclassification, which emphasized the importance of taking into account group membership probabilities when using these models (Stockburger 1998; Table 3). Most tracks were correctly classified in all models with probabilities $>90\%$, and most errors occurred in tracks classified as belonging to an incorrect group with low or medium probabilities.

The big canid versus big felid discriminant model (A1) and identification key (key 1) used size-independent variables; thus, their application apparently does not have limitations due to regional size variation. In addition, correct classification of both domestic dogs and maned wolf tracks as canids suggests application of discriminant model A1 and identification key 1 to differentiate big felid tracks from those of any large canid. We made a preliminary analysis with 6 coyote and 8 gray wolf tracks obtained from field guides of North American mammals (Childs 1998, Murie 1998, Paul and Gibson 2005, Reid 2006) and in all cases the classification key and A1 model correctly classified these tracks as canids (most of them with $>95\%$ membership probabilities). However, this method should be further evaluated with more tracks from these canid species where they could live in sympatry with pumas or jaguars.

In the comparison of puma versus jaguar models, we incorporated heel-pad width in model B1 as a variable directly related with track size as used by many authors (Fjelline and Mansfield 1988, Zielinski and Truex 1995, Childs 1998, Sharma et al. 2003). By excluding extreme-size tracks from training sets, we reduced the relative importance of track size, thereby improving overlapping-size track classification and overall classification success. The smallest jaguar tracks we used in the analysis had 4.99 cm and the biggest puma tracks had 7.46 cm total heel-pad width. Both of these tracks were correctly classified by model B1. Model B2 used a similar combination of variables but the exclusion of the heel pad diminished its classification accuracy.

In spite of the robustness and accuracy demonstrated by these models, differences between zoo and field tracks could be a source of error that we did not consider in our analysis. For this reason, when identification of a species is regarded as having high practical relevance (e.g., reporting a new locality for the species or needing to identify the predator in human-predator conflicts), we recommend having ≥ 2 tracks classified with medium or high probabilities of group membership ($>80\%$) before arriving at definitive conclusions. Additionally, given both the existence of track deformation that could lead to misclassification and the risk of several individuals from different species leaving tracks in the same place, we suggest measuring and classifying each track independently instead of using a mean value for a group of tracks (Zielinski and Truex 1995). Because of front and hind foot differences in puma and jaguar tracks (Brown and Lopez Gonzalez 2001), we suggest using as many tracks of a set as possible to compare membership assignment probabilities and have more

confidence in final decisions. Substrate type and track quality should also be considered in decisions; results from low-quality tracks should be taken with caution.

Animal age could also influence track classification when using key 2 and model B1, which are size-dependent. However, at the age of puma and jaguar dispersal (around 1.5–2 yr old; Sunquist and Sunquist 2002), most juveniles reach a size similar to an adult animal, particularly their paw size (Crawshaw 1995, Shaw et al. 2007). Juvenile tracks included in our analysis were correctly classified by key 2 and model B1. Considering the wide range of track size that we analyzed and the reduction of the relative importance of size made by excluding extreme-sized tracks, we feel confident that key 2 and model B1 should be useful with dispersing subadults' tracks. Key 3 and model B2, which are size-independent, could be an alternative method to avoid potential problems related with track size. Nevertheless, we suggest not using any of the keys and models with tracks <3.5 – 4 cm of pad width, to avoid confusion with younger animals and smaller canid or felid species not considered in our analysis. Tracks of kittens or predispersal pumas and jaguars will often be found with their mother's tracks, thus facilitating their track recognition (Shaw et al. 2007).

Our multivariate analyses present ≥ 2 main limitations in comparison with qualitative or univariate quantitative methods. First, some measurements are difficult to get, the process of obtaining them is time-consuming, and track digitalization is needed (i.e., total area and perimeter of the heel pad). Second, variable construction and discriminant function computation require mathematical skills. However, advanced technology and software are available for easy and precise image digitalization and for automatic calculations. Moreover, the digitalization process is facilitated by new methods for track collection (e.g., digital photographs or track-tracing and image scanner), and identification keys simplify the measurement and identification processes. We also incorporated the keys and models in a spreadsheet file uploaded as an online supplemental material related to this article at www.wildlifejournals.org (Supplemental material 1). Because we constructed identification keys by incorporating few measurements in each step and keys classified $>50\%$ of tracks (ensuring $>90\%$ of membership probabilities), we offer the spreadsheet as a guide to key use during the measurement process. It may also be helpful for the final models if the keys do not identify tracks, which does not necessarily make multivariate classification practical for field track identification, but it will help to reduce the time needed for arriving at confident classification results.

Unknown Track Identification

Qualitative and categorical traits performed well for track identification. In addition, qualitative criteria include not only features of isolated tracks, but also features of a trail of tracks from the same individual (e.g., Childs 1998, Hoogsteijn 2007, Shaw et al. 2007). However, these traits are subjective and their effectiveness frequently relies on high-quality track impressions and observer expertise

(Zielinski and Truex 1995, Lynam 2002, Sharma et al. 2003). Besides, finding good-quality tracks or complete track sets is difficult in some areas due to substrate condition and animal behavior (Sharma et al. 2003), and many surveys employ volunteers or students with low expertise in track recognition (e.g., Smallwood and Fitzhugh 1995, Wydeven et al. 2004, Danielsen et al. 2005, Markovchick-Nicholls et al. 2008, De Angelo 2009).

Multivariate track recognition using discriminant functions could be useful to solve problems related with poor-quality tracks and observer subjectivity, and has been successfully used to differentiate tracks of American martens (*Martes americana*) from tracks of fishers (*M. pennanti*; Zielinski and Truex 1995); those of mink (*Mustela vison*) from those of polecats (*Mustela putorius*; Harrington et al. 2008); claw marks of Asiatic black bears (*Ursus thibetanus*) from those of sun bears (*Helarctos malayanus*; Steinmetz and Garshelis 2008); and also for gender discrimination of tiger tracks (*Panthera tigris*; Sharma et al. 2003). Following a similar approach, we developed a robust multivariate classification method to recognize puma and jaguar tracks with confidence. Because we used tracks collected by different people in an unstandardized way, our method might be used to identify tracks obtained in the field from different sources and methods of collection. Additionally, selected variables and discriminant models may help to develop more accurate techniques for track differentiation in standardized track surveys in the future (e.g., when using smoothed plots; Wemmer et al. 1996). For example, a more detailed analysis using more tracks from each individual will improve ability for species differentiation, and independent classification of front and rear tracks may help to differentiate puma and jaguar tracks with more confidence. This approach could help to develop similar methods for male and female track identification of these species (Sharma et al. 2003), or for identifying other sympatric felid or canid species as well.

To apply our methods in unknown track samples from the field we suggest researchers 1) use keys and models in tracks with >4 cm of heel-pad width; 2) start with identification keys to distinguish tracks with confidence while using the minimum number of variables and mathematical calculation; 3) use complete discriminant models (Table 2) when identification keys do not classify the track; and 4) compare the resultant discriminant score with our classification results (Table 3) to get an estimate of confidence limits. In addition, we recommend using model B2 in areas where pumas are large (heel-pad width ≥ 7 cm) or jaguars are small (heel-pad width ≤ 5.50 cm) or when there is no information on track size (as in photographs obtained without a scale of reference).

MANAGEMENT IMPLICATIONS

Our multivariate classification method has ≥ 3 main applications in jaguar and puma conservation and management. First, our method offers a systematic approach for using jaguar and puma tracks with more confidence for surveying species presence, relative abundance, and habitat

use, without the need to rely on the opinion of experts in track identification. Secondly, tracks could be used with more confidence as a complementary source of information for research (e.g., helping in camera-trap localization) and conservation plans (e.g., detecting the use of biological corridors). Finally, tracks are often additional evidence collected for identifying predators in human-predator conflicts (Leite et al. 2002, Hoogesteijn 2007, Shaw et al. 2007). Tracks may not only help identify the species in attacks to livestock or humans, but also determine presence of potentially dangerous animals in urbanized or recreational areas. Management actions may differ depending on the predator species (puma, jaguar, or big canid); thus, correct track identification in these cases is extremely important.

ACKNOWLEDGMENTS

We thank Proyecto Yaguareté volunteers for their participation in the classification exercise and sample collection. We are grateful to M. Avalos, P. Brandolín, G. Boaglio, E. Catalá, L. Chiyo, A. Colmán, P. Cruz, W. de Moraes, Y. Di Blanco, J. Earnhardt, C. Ferrari, M. Guevara, M. Mealla, S. Moro, N. Perez, V. Quiroga, M. Ramírez, R. Rivero, C. Schloss, A. Sestelo, D. Villarreal, and all zoos' authorities and personnel for helping in track acquisition and processing. G. De Angelo and C. De Angelo gave us technical assistance in software management. L. Fitzhugh, R. Steinmetz, and Y. Jhala assisted with bibliography. We are thankful to J. Earnhardt, C. Boiero, E. Gese, S. Smallwood, D. Hanseder, and an anonymous reviewer for comments and suggestions for improving this manuscript. Financial support for this project was provided by National Research Council of Argentina (CONICET), Fundación Vida Silvestre Argentina, Education for Nature Program of the World Wildlife Fund (WWF), WWF-International, WWF-Switzerland, and Lincoln Park Zoo.

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APPENDIX A: QUALITATIVE TRAITS FOR TRACK DIFFERENTIATION

Big Canid and Big Felid Tracks

Summary of traits described by Smallwood and Fitzhugh (1989), Childs (1998), Brown and Lopez Gonzalez (2001) and Shaw et al. (2007). These criteria were mainly described for dogs and pumas, but most of these criteria are used for all big canid versus big felid track differentiation (see Fig. 1 for tracks comparison): 1) *Presence of claw marks*: canids have nonretractable claws so it is more common to find claw marks in the front of canid toes than in felid tracks; 2) *Relative size between toes and heel pad*: canids have bigger toes than felids in relation to the heel pad; 3) *Heel-pad size and shape*: canids have a triangular heel pad, usually with rounded front and with no-lobed or slightly bi-lobed back part. Felids have bigger and more squared or rounded heel pad, with a flatter or concave front part and tri-lobed back part; 4) *Toes' position*: the 2 middle toes (*ii* and *iii*) and the 2 outer toes (*i* and *iv*) of canid tracks tend to be in the same line and at the same distance to the heel pad, making the track nearly symmetric. Sometimes, this toe configuration shows an X shape in the space left by the toes and a mound of soil between toes and the heel. In felids, the second toe tends to be positioned more forward than the others, making nonsymmetric tracks; 5) *Outer toes' shape and direction*: felids' outer toes point to the front of the track. In canids, the first and the fourth toes usually point to the sides. In addition, canid outer toes usually show an angular shape in their inner edge, whereas those edges in felids' toes are more rounded; 6) *Pattern of tracks*: almost erratic in dogs but more regular and linear in felids.

Puma Versus Jaguar Track

Summary of features described by Schaller and Crawshaw (1980), Aranda (1994), Childs (1998), and Brown and Lopez Gonzalez (2001; see Fig. 1 for track comparison): 1) *Track size and shape*: jaguars have bigger and more rounded tracks than pumas; 2) *Heel-pad size and shape*: jaguars have more rounded and bigger heel pad than pumas. Pumas have 3 prominent lobes in the base of the heel pad that are less pronounced in jaguars. The middle lobe should be wider in jaguar heel pads; 3) *Toes' shape and position*: jaguars have more rounded toes, but puma toes are more elongated and pointed. Jaguar toes are positioned around the heel pad. Puma toes tend to be farther from the heel pad.

APPENDIX B: EXISTING QUANTITATIVE CRITERIA

Summary of quantitative criteria described in the literature for dogs versus pumas and puma versus jaguar track differentiation (see Fig. 1 for track comparison):

Dog Versus Puma Tracks

Belden (1978).—Ratio of the width of the widest toe to the heel pad (see Fig. 1: max. between b_{1i} – b_{4iv} divided by a_1): if the ratio exceeds 0.44 the track belongs to a dog, and below 0.44 the track belongs to a puma.

Smallwood and Fitzhugh (1989).—Angle formed by the longitudinal axis of the 2 outer toes (*Angle D* in Fig. 1): if the angle is $\leq 29^\circ$, the track probably belongs to a puma, if the angle is $\geq 30^\circ$, the track is most likely from a dog (following modifications proposed for this criterion by Shaw et al. 2007). To construct this range, Smallwood and Fitzhugh (1989) used 19 dog tracks and 48 puma tracks identified in the field by qualitative criteria.

Shaw et al. (2007).—Even young puma kittens have a heel-pad width of ≥ 3.5 cm (a_1 in Fig. 1). Tracks with < 3.5 cm of heel-pad width are most likely from smaller felid species or from dogs.

Puma Versus Jaguar Tracks

Aranda (1994).—Any of the toes is divided into thirds. The width at one-third is divided by the width at two-thirds (see Fig. 1: b_3 divided by b_4 for any of the toes i – iv). Confidence limits range from 0.71 to 1.03 for jaguar and 0.60 to 0.76 for puma. Values > 0.76 mean jaguar track and values < 0.71 mean puma track, with an undefined range of 0.71–0.76. Aranda (1994) used 10 tracks from 2 captive jaguars and 8 tracks from 2 captive pumas, plus 70 jaguar and 45 puma tracks from the field (Mexico) identified by qualitative criteria.

Childs (1998) a.—Percent ratio of heel-pad square area (width \times length), to total track square area of the rear track (*VarB8* in Appendix C). Jaguar range = 41.2–56.7%, puma range = 28.1–38.5%. Childs (1998) described this range using 15 jaguar and 8 puma tracks from the field (Pantanal, Brazil) identified by qualitative criteria, but there is no information about the number of rear tracks out of the total.

Childs (1998) b.—This author suggests that maximum width of rear feet heel pad (a_1 in Fig. 1) could be useful to differentiate species and shows the range from Pantanal (Brazil) tracks: jaguar = 7.0–8.8 cm, puma = 4.5–7.0 cm. Brown and Lopez Gonzalez (2001) also mentioned this criterion and provided data from Southern United States and Northern Mexico: jaguar 5.1–8.9 cm, puma 4.1–5.6 cm. Shaw et al. (2007) mention values between 4.1 cm and 6.3 cm for puma rear tracks from Arizona and California, USA. Childs (1998) described this range using 15 jaguar and 8 puma tracks from the field (Pantanal, Brazil) identified by qualitative criteria, but there is no information about the number of rear tracks out of the total. Brown and Lopez Gonzalez (2001) and Shaw et al. (2007) do not mention the source of their information.

APPENDIX C: VARIABLE DESCRIPTIONS

Description of variables incorporated in discriminant models and identification keys using measurements from Figure 1. We used these variables with tracks from dogs, maned wolves,

pumas, and jaguars, collected from 18 zoos from Argentina, Brazil, Colombia, Paraguay, United States, and Venezuela, and urban areas from Argentina, 2004–2008. We included the complete list of evaluated measurements and variables in the Online Supplemental Material 2 (Fig. S1 and Table S1) uploaded as online supplemental material of this article at <www.wildlifejournals.org>.

VarA1.—Width at the third quarter of the heel pad (total length of the heel pad needed), divided by total heel-pad width:

$$\text{VarA1} = a3 / a1$$

VarA2.—Average of toe total width, divided by heel-pad total width (modified from Belden 1978):

$$\text{VarA2} = [(b1i + b1ii + b1iii + b1iv) / 4] / a1$$

VarA3.—Reciprocal transformation of *VarA2*:

$$\text{VarA3} = 1 / \text{VarA2}$$

Angle X.—See Figure 1.

VarB1.—Natural logarithm of heel-pad total width:

$$\text{VarB1} = \ln(a1)$$

VarB2.—Cubic transformation of the heel-pad shape factor described by Lewison et al. (2001):

$$\text{VarB2} = [(4 \times \pi \times a4) / (a5^2)]^3$$

VarB3.—Average of the first third width divided by second third width of each toe (modified from Aranda 1994):

$$\text{VarB3} = [(b3i / b4i) + (b3ii / b4ii) + (b3iii / b4iii) + (b3iv / b4iv)] / 4$$

VarB4.—Square transformation of *VarB3*:

$$\text{VarB4} = (\text{VarB3})^2$$

VarB5.—Actual area of the heel pad divided by the squared area of the track (total track width \times total track length) expressed as percentage:

$$\text{VarB5} = [a4 / (c1 \times c2)] \times 100\%$$

VarB7.—The higher distance between toes and the heel pad divided by the heel-pad width:

$$\text{VarB7} = b5 / a1$$

VarB8.—Squared area of the heel pad divided by the squared area of the track, expressed as percentage (from Childs 1998):

$$\text{VarB8} = [(a1 \times a2) / (c1 \times c2)] \times 100\%$$

VarB9.—Mean of length:width ratio of toes 2 and 3:

$$\text{VarB9} = [(b2ii / b1ii) + (b2iii / b1iii)] / 2$$

Associate Editor: Gesé.