

## Original Article

# Using Shape and Size to Quantify Variation in Footprints for Individual Identification: Case Study With White Rhinoceros (*Ceratotherium simum*)

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**ABSTRACT** For those vertebrate species that create sufficiently complex footprints, identifying individuals from their footprints promises to be a noninvasive technique of great potential for wildlife studies and conservation, but with statistical challenges. Various approaches to employing footprints for identification appear in the literature, but doubt often remains as to the information contained in the footprints and therefore of the reliability of the procedures. For footprints represented by landmarks, we propose using pre-assigned measures of shape and size of configurations of landmarks to quantify the variation in footprints amongst individuals relative to the variation in each individual's footprints. Our method provides a relatively simple means of assessing when footprints (represented by landmarks) from individuals of a population will be useful for identifying individuals, independent of any particular identification algorithm, and is also a tool for exploring footprint landmark data to aid development of discrimination routines. We illustrate the method using footprints collected from a population of white rhinoceros (*Ceratotherium simum*) at Otjiwa Game Ranch, Namibia, during late 1999. © 2013 The Wildlife Society.

**KEY WORDS** *Ceratotherium simum*, footprint-based identification, individual-based studies, monitoring, rhinoceros, size and shape.

Identification of individual animals from physical features is of great value in wildlife and conservation studies and has been an essential ingredient of many field studies and monitoring programs. Examples for terrestrial vertebrates include exploiting coat patterns (e.g., Smith et al. 1999, Kelly 2001, Karanth et al. 2006, Foster et al. 2007) and the mystacial vibrissae spot patterns of felids (Pennycuik and Rudnai 1970, Miththapala et al. 1989). Though such methods are not without challenges (e.g., subjective elements in protocols, errors of misidentification) they largely sidestep concerns raised by invasive monitoring techniques (Murray and Fuller 2000, Tuytens et al. 2002, Moorhouse and MacDonald 2005). Of most interest are attempts to produce pattern recognition algorithms that are objective and can be automated.

Utilizing natural marks still requires locating individuals, however, either by observer or remote sensing (e.g., camera traps). Location and re-location, is particularly difficult for species occurring at low densities, and/or that are reclusive,

shy, and/or nocturnal. Animals that leave tracks in suitable substrate produce potentially valuable data (e.g., regarding density, location, movement), which can be exploited without re-locating (or possibly even locating) the individual itself if it can be identified by its footprints (Stander et al. 1997). Exploiting footprints, however, poses its own challenges due to the variation in footprints of an individual, largely as a function of variation in substrate, but also due to variation in gait and degradation of footprints with time or from disturbance. While the latter issues can be addressed by suitable protocols of footprint collection, the former is essentially a statistical issue that must be addressed for any identification technique based on footprints. Although there have been various attempts to utilize footprints, some have been criticized for not addressing the relevant statistical concerns (notably by Karanth et al. 2003), and some have not been developed adequately as field tools (but see Sharma et al. 2005). We have developed a footprint identification technique we call FIT, initially for black rhinoceros (*Diceros bicornis*; Jewell et al. 2001), refined with white rhinoceros (*Ceratotherium simum*; Alibhai et al. 2008), and developed further through application to a range of other species (see [www.wildtrack.org](http://www.wildtrack.org)).

In the absence of a model of the basis of discrimination from which performance can be derived, an automated

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identification technique exploits training data to drive algorithm construction to discern difference between individuals, possibly against a background of individual variation. The algorithm is then validated using independent test data. Satisfactory performance of the algorithm is typically regarded as license to employ the algorithm at least for the population that provided the training and test data, though the definition of that population might be unclear. Without a model of the variation in the feature in question, however, no inference, logical or statistical, can be drawn regarding the performance of the algorithm beyond the training and test sets.

All nonparametric pattern-recognition techniques face this challenge. Application of algorithms beyond their training and test data appears to be justified typically by plausibility arguments, supported perhaps by further testing. Algorithms built with statistical techniques (e.g., FIT), often result in rules of discrimination that are not readily interpretable in terms of the data, making it difficult, for example, to understand failures of discrimination. With FIT, a footprint is represented by landmarks, that is, a collection of points on the footprint that can be systematically located on any footprint by a specified algorithm (e.g., as in Jewell et al. 2001, Alibhai et al. 2008; Fig. 1). Our aim in this article is to employ readily interpretable pre-assigned properties of footprints represented by landmarks to quantify variation in footprints and thereby provide a protocol for assessing, for

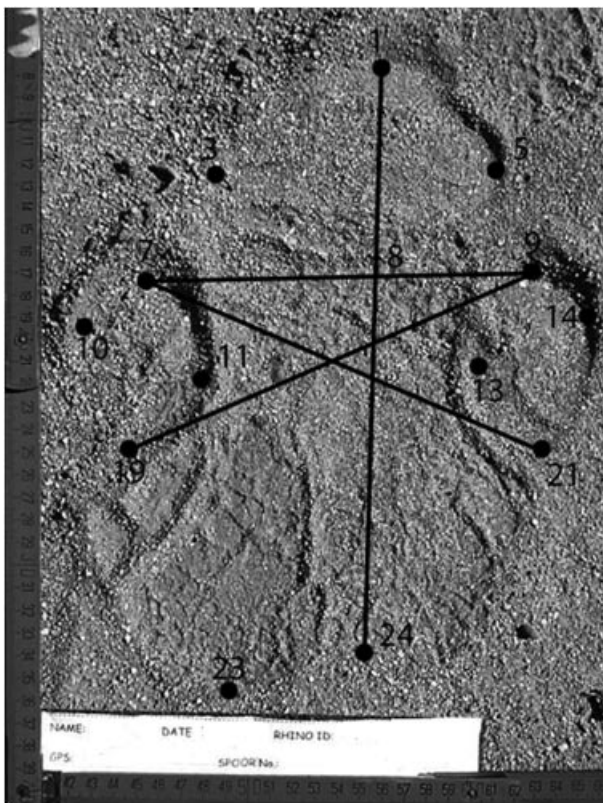
a given set of footprints from known individuals, the within-identity- and amongst-identity-variation between footprints. This protocol provides an exploratory tool for assessing the suitability of footprints represented by landmarks for individual identification (or other discrimination, such as sex; Sharma et al. 2003) and a means for exploring, using these footprint properties, the underlying reasons for failures of discrimination by an algorithm.

## STUDY POPULATION AND DATA

Our study population consisted of the white rhinoceros present on the Otjiwa Game Ranch, near Otjiwarongo, Namibia, in late 1999. The ranch is a fenced area of approximately 100 km<sup>2</sup> of mostly flat ground with substantial areas of sandy substrate in open terrain and game trails through predominantly acacia bushveld. The ranch has multiple artificial water points; mean annual rainfall is around 500 mm.

Permission for the project was provided by the Ministry of Environment and Tourism of Namibia; no animals were handled for this work. Our team, in conjunction with anti-poaching units, intensively tracked and observed individuals over 6 weeks in October and November prior to the summer rains. To reduce variation in an individual's footprint, we only photographed footprints with a clear outline and that resulted from a walking gait on level ground. In a walking gait a (white) rhinoceros typically registers its hind foot over the footprint of its front foot, so we photographed only hind footprints and arbitrarily selected left hind; all subsequent references to "footprint" refer to left hind footprint and indicate either an actual footprint or a digital photograph of the footprint. Apart from these constraints, we photographed as many footprints as possible to reflect the natural variation in footprints. No isolated single footprints were photographed, however, but only footprints belonging to a continuous sequence of footprints, referred to as a "trail."

Several rhinoceroses were identifiable from physical features (horn size and shape) and had been named by the ranch managers, but we needed an objective method for assigning trails to all individuals. Cracks in the plantar pad of the feet result in ridges within the footprint (Fig. 1). The patterns of these ridges remained consistent over the field season, could be reliably distinguished by independent observers either in the field or in photographs, and led researchers consistently to the same individual in the field (identified by a combination of individual physical features and membership in stable social groups). This method of identifying rhinoceros has also been employed independently (Brett et al. 1989). Ultimately, we could visually identify 26 individual rhinoceroses from their footprints, and data collection during the study produced no trails that could not be assigned to a known individual, despite systematic searching of the enclosed game ranch. We concluded that the population consisted of 2 mature males (J and M), 7 breeding females (G, W, F, S, T, K, and B), and 17 immature individuals, each of which was a calf of one of the breeding females with a maternal identity asserted by the ranch managers based on daily monitoring conducted by the anti-poaching units. We adopted the assigned names of the immature animals,



**Figure 1.** Footprint showing a ridge pattern, which permitted identification of individual white rhinoceroses, and the landmarks placed on each footprint. Footprints were collected at Otjiwa Game Ranch, Namibia, during late 1999.

and used the symbol of their reputed mother and a numeral indicating their birth order (e.g., G2 is the presumed second-oldest calf of G). The validity of the maternal attributions of the immature animals was irrelevant to this study (but see Supplement, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

Our data set consisted of footprints obtained from trails that could be unambiguously assigned to an identified rhinoceros and for which the landmarks utilized in FIT (Fig. 1) could be placed. The data set consisted of 961 footprints, distributed among the rhinoceroses as follows. G: 41; G1: 58; G2: 29; G3: 16; W: 42; W1: 44; W2: 37; B: 32; B1: 10; K: 22; K2: 40; K3: 47; K4: 36; F: 21; F1: 70; F3: 21; S: 27; S1: 21; S2: 42; S3: 15; T: 49; T1: 31; T2: 39; T3: 36; M: 108; J: 27.

## METHODS

Footprints were collected from trails to ensure unambiguous identification, but the trail grouping itself plays no role in our analyses. Trail grouping may be utilized in identification algorithms, as in FIT, but that is irrelevant to our purposes here for which individual footprints are the unit of interest and the 961 footprints the population of interest. Our aim is to quantify variation among these 961 footprints relative to the known rhinoceros identities. Hence, there are no issues of pseudo-replication.

We used insights from the application of FIT to rhinoceros footprints (Jewell et al. 2001, Alibhai et al. 2008) to select the landmarks that would represent the footprints for the analyses of this article, namely the landmarks numbered 1, 3, 5, 7, 9, 10, 11, 13, 14, 19, and 21, which represent the geometry of the 3 toes, in Figure 1 (see Jewell et al. 2001 or the supplement for rules of landmark placement). Although our choice of landmarks takes advantage of FIT, the procedure described in this article could be employed to help select suitable landmarks during algorithm construction.

The horizontal line through landmarks 7 and 9, together with the perpendicular line through landmark 1, provide Cartesian axes, with scale provided by the ruler. Hence, each landmark has Cartesian coordinates and the footprint is thereby represented as a configuration of 11 points in the Euclidean plane. We desired pre-assigned, objective measures, with transparent interpretations, of the landmark configuration. Natural definitions of shape and size of landmark configurations in the plane are available that promise to meet our goals (Kendall 1984; see the online Supplement for an outline). If  $(x_1, y_1), \dots, (x_n, y_n)$  are the  $n$  landmarks representing a footprint configuration, let  $(x_0, y_0)$  be the mean, called the “centroid” of the configuration. The “centroid size” of the configuration is defined by

$$S := \sqrt{\sum_{j=1}^n (x_j - x_0)^2 + (y_j - y_0)^2}$$

For each landmark of a footprint configuration, one subtracts the centroid and divides by the centroid size to obtain a mean-centered and scaled representation of the configura-

tion. Now let  $(x_1, y_1), \dots, (x_n, y_n)$  and  $(u_1, v_1), \dots, (u_n, v_n)$  represent 2 configurations ( $P$  and  $Q$ , respectively) that have already been mean-centered and scaled. The “Kendall distance” between the shapes of these 2 configurations is given by

$$d(P, Q) = \cos^{-1} \sqrt{\left[ \sum_{j=1}^n (x_j u_j + y_j v_j) \right]^2 + \left[ \sum_{j=1}^n (y_j u_j - x_j v_j) \right]^2}$$

These 2 simple formulae allow one to compare sizes and shapes of configurations.

One could begin with a traditional principal component analysis of inter-landmark distances to assess the relative contributions of size and shape to the variation in the data set (see the online Supplement for details), but we will focus on the analysis of centroid size and shape using the above formulae. Our analysis of footprint size is a standard statistical analysis of the logarithm  $\ln(S)$  of centroid size with rhinoceros identity as factor. For shape analysis, the set of 11 landmarks of each footprint was converted to a mean-centered configuration scaled to unit centroid size and the Kendall distance between the shapes of all pairs of footprints computed and taken as a measure of dissimilarity. The space of shapes is nonlinear, so we used nonmetric multidimensional scaling (nMDS) as an exploratory tool of this dissimilarity and ANOSIM (Clarke 1993, Clarke and Warwick 2001) to quantify shape difference between footprint configurations. ANOSIM is a permutation test that returns a statistic  $R_0$  that is approximately zero when there is no relation between similarity between points (here, shapes) and group identity (here, rhinoceros identity) and that approaches one as group identity determines similarity. See the online Supplement for details.

## RESULTS

For the size analysis, we were able to apply ANOVA and the Tukey–Kramer test for unequal group size for post hoc multiple comparisons (using JMP 5; SAS Institute, Inc., Cary, NC) after excluding the 3 smallest calves (K4, T3, and B1), whose footprints were unambiguously smaller than all others; Welch’s  $t$ -test sufficed to test the only two of these (K4 and T3) whose footprints overlapped in size (see the online Supplement for details). Table 1 records, for each rhinoceros, those rhinoceroses that could not be distinguished from that rhinoceros by size of footprint configuration.

Figures 2 and 3 exhibit, respectively, the extremes of excellent separation (for F1 and T3) and failure of separation (F1 and S1; in Figure 3 we show a plot derived from a nine-dimensional nMDS in order to show the failure of separation with the minimum stress obtained). The extremely good separation in Figure 2 is unsurprising given the obvious difference in shape between the footprints of small calves (T3; more rounded) and larger animals (more elongated) but was also obtained for various pairs of adults. In many cases, such clean separation was spoiled only by a few points that behaved as outliers in most plots.

**Table 1.** The table lists each white rhinoceros in the study (Otjiwa Game Ranch in late 1999) against the white rhinoceroses in the study that were not distinguished from the listed rhinoceroses by footprint size.

Rhino	Other rhinos the listed rhino was not distinguished from by footprint size	Rhino	Other rhinos the listed rhino was not distinguished from by footprint size
G	W; F1; S; T1; T2; J	F1	G; W; S; T1; T2; J
G1	W1; S; T2; J	F	G2; G3; K2; K3; S2; T
G2	W2; B; K; K2; K3; F; S1; T	F3	S3
G3	K2; F; S2	S	G; G1; W1; F1; T1; T2; J
W	G; F1; T1	S1	G2; W1; W2; B; K; M
W1	G1; B; K; S; S1; M	S2	G3; K2; F
W2	G2; B; K; K3; S1	S3	F3
B	G2; W1; W2; K; S1; M	T	G2; K2; K3; F
B1		T1	G; W; F1; S; T2; J
K	G2; W1; W2; B; S1; M	T2	G; G1; F1; S; T1; J
K2	G2; G3; K3; F; S2; T	T3	
K3	W2; G2; K2; F; T;	M	W1; B; K; S1
K4		J	G; G1; F1; S; T1; T2

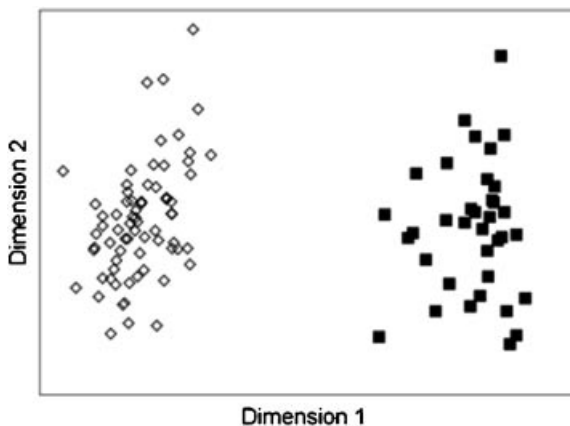
The ANOSIM on all footprint configuration shapes with rhinoceros identity as factor returned an  $R_0$  value of 0.74, which was also the extreme value for the distribution obtained from 9,999 randomly chosen permutations, and the groups were considered different at a level of significance of  $P = 0.0001$ .

ANOSIM also provides a post hoc multiple comparison of all pairs. For each pair, 9,999 permutations were performed and, other than for the pair (F1, S1), the observed  $R_0$  was the most extreme value obtained and, hence, significant at  $P = 0.0001$ ; for (F1, S1), 6 of the 9,999 permutations yielded an  $R$  value at least as great as the  $R_0$  value obtained for this pair. Employing the Bonferroni correction, all pairs, except (F1, S1), were regarded as different while maintaining a probability of a Type I error of 0.05 when considering all 325 distinct pairs simultaneously.

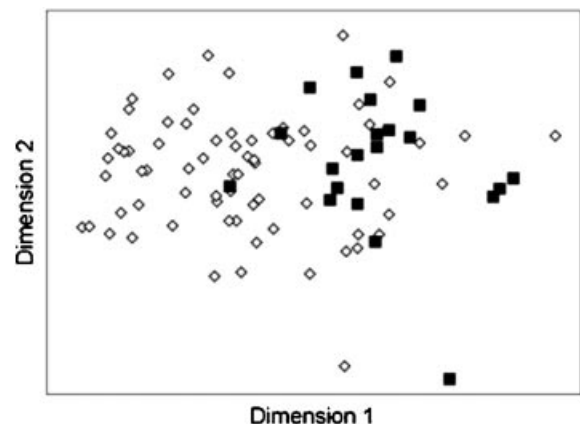
Figure 4 records the frequency distribution of observed  $R_0$  values for the 325 pairwise comparisons. The mean observed

$R_0$  value was 0.826, with (population) standard deviation of 0.173; the median was 0.872; and the mode was 0.996. Most rhinoceros pairs have high values of  $R_0$ , which indicates substantial separation of footprint configuration shapes by rhinoceros identity, and only for (F1, S1) is there a statistical failure to discriminate between the rhinoceroses. The  $R_0$  value 0.223 for the pair (F1, S1) was the smallest, the next smallest being 0.227 for the pair (G1, T). Figures 3 and 5 do exhibit a qualitative difference in the degree of separation, which is quantified by ANOSIM. Any difference between F1 and S1 appears to be just beyond what ANOSIM could distinguish in this data set.

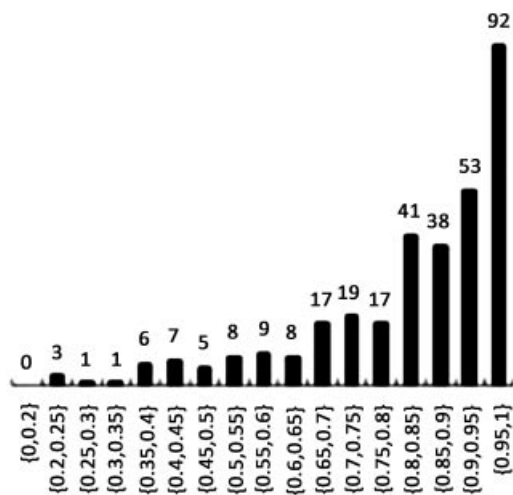
We note that of the 92 pairs with  $R_0$  in  $[0.95, 1]$ , 61 are pairs for which one rhinoceros is one of the small calves K4, T3, or B1; another 20 involve one of the larger calves F3 or K3. Our perception of the difference in shape of footprints between younger and older animals is therefore borne out by the analysis. For (T3, K4),  $R_0 = 0.274$ ; but for (B1, T3) and



**Figure 2.** The 2-dimensional projection, with greatest separation between groups, of a 4-dimensional nonmetric multidimensional scaling plot (stress = 0.05) of shapes of footprint configurations for the adult F1 (open diamonds) and calf T3 (solid squares). The analogous 2-dimensional projection of a 9-dimensional nonmetric multidimensional scaling plot (stress = 0.021) is little different. Footprints were collected at Otjiwa Game Ranch, Namibia, during late 1999.



**Figure 3.** The 2-dimensional projection, with greatest separation between groups, of a 9-dimensional nonmetric multidimensional scaling plot (stress = 0.040) of shapes of footprint configurations for the two subadult females F1 (open diamonds) and S1 (solid squares), the only two rhinoceros identities not distinguished by ANOSIM. Footprints were collected at Otjiwa Game Ranch, Namibia, during late 1999.



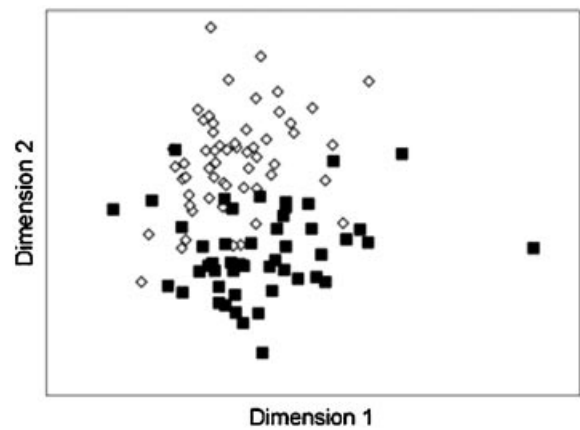
**Figure 4.** Frequencies of observed ANOSIM  $R_0$  values for all 325 rhinoceros pairs, comparing footprint configuration shapes. Range of observed  $R_0$  values is the closed interval  $[0,1]$ , divided on the  $x$ -axis into semi-closed/open intervals, for example,  $[0.5,0.55)$ , meaning  $0.5 \leq R_0 < 0.55$ . Footprints were collected at Otjiwa Game Ranch, Namibia, during late 1999.

(B1, K4),  $R_0 = 0.734$  and  $0.711$ , respectively. Of the 23 pairs with  $R_0 < 0.5$ , only 3 are not distinguished by size: (K, S1),  $R_0 = 0.422$ ; (G, T1),  $R_0 = 0.438$ ; (F, S2),  $R_0 = 0.44$ .

## DISCUSSION

Identifying individuals using body features (e.g., coat patterns as referenced in the introduction, and outlines of flukes, fins, and flippers of marine mammals) that are sufficiently distinct amongst study individuals also requires identifying variation in photographic images of the body feature of each individual, which is aided by the fact that each individual has, in principle, an ideal image of the body feature as a standard (e.g., variation in images of whale flukes due to variation in the angle of the plane in which the fluke lies when photographed may be accounted for because each image is a geometric transformation of the ideal; Kniest et al. 2010).

Footprints, however, result from the dynamic interaction of the foot in motion with varying substrate, and there is no ideal image for comparison. Rather, there is the statistical challenge of quantifying individual variation in footprints against variation between individuals. For footprints represented by landmarks, we have shown how well-defined measures of size and shape can be exploited for this purpose. Experience with FIT ([www.wildtrack.org](http://www.wildtrack.org)) indicates that species amenable to individual identification from their footprints include, in addition to rhinoceros, tapir (Tapiridae), bears (Ursidae), and a variety of carnivores with substantially smaller footprints than rhinoceros (tiger *Panthera tigris*, cheetah *Acinonyx jubatus*, striped hyena *Hyaena hyaena*). The method presented in this article is equally relevant to any landmark-based footprint identification scheme (e.g., Riordan 1998; Grigione et al. 1999; Sharma et al. 2003, 2005); these and other studies (e.g., Lizcano and Cavalier 2000, Isasi-Catalá and Barreto 2008) have provided further evidence for the applicability of footprint-based identifica-



**Figure 5.** The 2-dimensional projection, with greatest separation between groups, of a 9-dimensional nonmetric multidimensional scaling plot (stress = 0.05) of shapes of footprint configurations for the female subadult G1 (open diamonds) and female adult T (solid squares), the pair of rhinoceroses with the smallest  $R_0$  value for which ANOSIM distinguished the pair of rhinoceroses. Footprints were collected at Otjiwa Game Ranch, Namibia, during late 1999.

tion to various felids and tapir; canids should be equally suitable.

Our analyses were conducted without pruning of data and with considerable variation in sample sizes for different rhinoceroses. Enhanced performance can be expected by stipulating minimum sample sizes (based on experience to date, we suggest  $\geq 25$  footprints/individual) and removing outliers; nMDS plots are particularly useful for exposing outliers. Once experience has been gained with footprints of the study species, careful selection of footprints in the field will also decrease individual variation in footprints.

An important question is the “resolving power” of a given discrimination technique. Assuming the technique is based on essentially continuous variables, in how large a population can one expect the technique to distinguish all individuals? For ecological applications, however, one does not need to discriminate individuals whose spatial ranging does not overlap, so in practice the theoretical limits of discrimination may not be relevant, though further research on this issue is required.

## MANAGEMENT IMPLICATIONS

Identifying individuals, especially of reclusive, nocturnal, or rare species, from their footprints promises a noninvasive, cost-effective, technique for monitoring and research. Confirming suitability of a species and developing a successful algorithm are the main challenges to employment of footprints. Size and shape are readily interpretable features that can be exploited to address the former and assist with the latter challenge.

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## LITERATURE CITED

- Alibhai, S. K., Z. C. Jewell, and P. R. Law. 2008. A footprint technique to identify white rhino *Ceratotherium simum* at individual and species levels. *Endangered Species Research* 4:205–218.
- Brett, R. A., J. K. Hodges, and E. Wanjohi. 1989. Assessment of reproductive status of the black rhinoceros (*Diceros bicornis*) in the wild. Pages 147–161 in E. D. Bergmann and G. M. O. Maloiy, editors. *The biology of large African mammals in their environment*. Symposia of the Zoological Society of London 61, Clarendon Press, Oxford, England, United Kingdom.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Clarke, K. R., and R. M. Warwick. 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. Second edition. PRIMER-E, Plymouth Marine Laboratory, Plymouth, Devon, England, United Kingdom.
- Foster, G., H. Kijger, and S. Bangay. 2007. Towards a computer-aided identification system for individual zebra. *African Journal of Ecology* 45:225–227.
- Grigione, M. M., P. Burman, V. C. Bleich, and B. M. Pierce. 1999. Identifying individual mountain lions *Felis concolor* by their tracks: refinement of an innovative technique. *Biological Conservation* 88:25–32.
- Isasi-Catalá, E., and G. R. Barreto. 2008. Identificación de individuos de jaguars (*Panthera onca*) y pumas (*Puma concolor*) a partir de morfometría de sus huellas (Carnivora: Felidae). *Revista de Biología Tropical* 56:1893–1904.
- Jewell, Z. C., S. K. Alibhai, and P. R. Law. 2001. Censusing and monitoring black rhino (*Diceros bicornis*) using an objective spoor (footprint) identification technique. *Journal of Zoology London* 254:1–16.
- Karanth, K. U., J. D. Nichols, N. S. Kumar, and J. E. Hines. 2006. Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology* 87:2925–2937.
- Karanth, K. U., J. D. Nichols, J. Seidensticker, E. Dinerstein, J. L. D. Smith, C. McDougal, A. J. T. Johnsingh, R. S. Chundawat, and V. Thapar. 2003. Science deficiency in conservation practice: monitoring of tiger populations in India. *Animal Conservation* 6:141–146.
- Kelly, M. J. 2001. Computer-aided photographic matching in studies using individual identification: an example from Serengeti cheetahs. *Journal of Mammalogy* 82:440–449.
- Kendall, D. G. 1984. Shape manifolds, procrustean metrics, and complex projective spaces. *Bulletin of the London Mathematical Society* 16: 81–121.
- Kniest, E., D. Burns, and P. Harris. 2010. Fluke Matcher: a computer-aided matching system for humpback whales (*Megaptera novaeangliae*) flukes. *Marine Mammal Science* 26:744–756.
- Lizzano, D. J., and J. Cavalier. 2000. Densidad polacionad y disponibilidad de habitat de la dantade Montana (*Tapirus pinchque*) en los Andes centrales de Colombia. *Biotropica* 32:165–173.
- Miththapala, S., J. Seidensticker, L. G. Phillips, S. B. U. Fernando, and J. A. Smallwood. 1989. Identification of individual leopards (*Panthera pardus kotiya*) using spot pattern variation. *Journal of Zoology London* 218:527–536.
- Moorhouse, T. P., and D. W. MacDonald. 2005. Indirect negative impacts of radio-collaring: sex ratio variation in water voles. *Journal of Applied Ecology* 42:91–98.
- Murray, D. L., and M. R. Fuller. 2000. A critical review of the effects of marking on the biology of vertebrates. Pages 15–64 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, New York, USA.
- Pennycuik, C. J., and J. Rudnai. 1970. A method of identifying lions, *Panthera leo*, with an analysis of the reliability of identification. *Journal of Zoology London* 160:497–508.
- Riordan, P. 1998. Unsupervised recognition of individual tigers and snow leopards from their footprints. *Animal Conservation* 1:253–262.
- Sharma, S., Y. Jhala, and V. B. Sawarkar. 2003. Gender discrimination of tigers by using their pugmarks. *Wildlife Society Bulletin* 31:258–264.
- Sharma, S., Y. Jhala, and V. B. Sawarkar. 2005. Identification of individual tigers (*Panthera tigris*) from their pugmarks. *Journal of Zoology London* 267:9–18.
- Smith, J. L. D., C. McDougal, S. C. Ahearn, A. Joshi, and K. Conforti. 1999. Metapopulation structure of tigers in Nepal. Pages 176–191 in J. Seidensticker, S. Christie, and P. Jackson, editors. *Riding the tiger: tiger conservation in human-dominated landscapes*. Cambridge University Press, Cambridge, England, United Kingdom.
- Stander, P. E., // Ghau, D. Tsisaba, // †. Oma, and // U. 1997. Tracking and the interpretation of spoor: a scientifically sound method in ecology. *Journal of Zoology London* 242:329–341.
- Tuytens, F. A. M., D. W. MacDonald, and A. W. Roddam. 2002. Effects of radio-collars on European badgers (*Meles meles*). *Journal of Zoology London* 257:37–42.

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