

Dietary separation of sympatric carnivores identified by molecular analysis of scats

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Abstract

We studied the diets of four sympatric carnivores in the flooding savannas of western Venezuela by analysing predator DNA and prey remains in faeces. DNA was isolated and a portion of the cytochrome *b* gene of the mitochondrial genome amplified and sequenced from 20 of 34 scats. Species were diagnosed by comparing the resulting sequences to reference sequences generated from the blood of puma (*Puma concolor*), jaguar (*Panthera onca*), ocelot (*Leopardus pardalus*) and crab-eating fox (*Cerdocyon thous*). Scat size has previously been used to identify predators, but DNA data show that puma and jaguar scats overlap in size, as do those of puma, ocelot and fox. Prey-content analysis suggests minimal prey partitioning between pumas and jaguars. In field testing this technique for large carnivores, two potential limitations emerged: locating intact faecal samples and recovering DNA sequences from samples obtained in the wet season. Nonetheless, this study illustrates the tremendous potential of DNA faecal studies. The presence of domestic dog (*Canis familiaris*) in one puma scat and of wild pig (*Sus scrofa*), set as bait, in one jaguar sample exemplifies the forensic possibilities of this noninvasive analysis. In addition to defining the dietary habits of similar size sympatric mammals, DNA identifications from faeces allow wildlife managers to detect the presence of endangered taxa and manage prey for their conservation.

Keywords: carnivore feeding ecology, diet, faecal DNA, Felidae, species diagnosis

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Introduction

The jaguar (*Panthera onca*) and puma (*Puma concolor*) are sympatric across much of the Neotropics. Both are endangered, primarily because of habitat loss and persecution prompted by depredation on livestock. Understanding the dietary habits of these felids will aid conservation efforts by clarifying prey preferences in natural and disturbed areas and documenting the impact of felid predation on livestock mortality.

Scats (faeces) provide a valuable sample of carnivore diets, but where several similar size carnivores co-occur, reliable identification of the correct donor species has been a substantial impediment to dietary analysis. Although previous studies have demonstrated that epithelial cells

from the colon wall, sloughed off and deposited in scats, are a reliable source of DNA to determine species of origin (e.g. Höss *et al.* 1992; Paxinos *et al.* 1997; Wasser *et al.* 1997), this technique has rarely been field tested on samples of unknown species origin. Here we present the first use of molecular scatology to analyse the dietary habits of sympatric carnivores.

We developed a molecular assay based on mtDNA sequences to identify predator species from scats and assess the general utility of species identification with scat-derived DNA. An mtDNA test was chosen over parallel nuclear DNA assays because each diploid cell contains hundreds or thousands of copies of mtDNA, compared with two copies of nuclear DNA. These multiple copies should be easier to recover from samples that are partially degraded, and mtDNA coding regions offer an appropriate range of resolution; even relatively short sequences reveal diagnostic differences between carnivore

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species. We chose the cytochrome *b* gene because it is one of the most widely applied regions of the mitochondrial genome for phylogenetic comparisons (Jones & Avise 1998).

To define the dietary habits of pumas and jaguars it was necessary to identify prey contents from a wide range of scat sizes. Scat diameter is the prevalent way of assigning prey items to species. However, there are reasons to doubt the accuracy of assignments based on size. Although the average body weight of carnivores such as ocelots (10 kg), pumas (40–50 kg) and male jaguars (100 kg) varies greatly, scats of large and small carnivores may be similar in size. We have found puma scats smaller than 20 mm in diameter and ocelot scats of up to 27 mm in diameter. This overlap shows that a technique more reliable than scat size is required in order to identify predators. Genetic identification of scats can provide accurate dietary analysis, pinpoint problem carnivores near ranches and human settlements, and help design wildlife reserves and corridors.

Methods

Prey identification

Carnivore faecal samples were collected during a radio-telemetry study of pumas and jaguars at Hato Piñero, Cojedes, Venezuela, in 1996. Samples were gathered opportunistically, primarily along roads and trails on this 80 000 hectare cattle ranch with extensive areas of natural habitat on the flooding savannas, or llanos, of western Venezuela. Only scats containing animal remains were used in the analysis. Of 239 collected scats, 70 were suspected to be from large felids. Each scat was air dried on sterile paper in fine-mesh wire cages. Cages were rinsed with ethanol and flame-sterilized between samples. Dried scats were measured, then gently pulled apart, and the bile powder sifted away from the prey contents. Prey remains were visually identified to the lowest taxon possible by examining teeth, claws, bones, fur, feathers and scales. The presence of plant material was noted. Bile powder was stored in new Ziploc bags in a dark, dry location during the field season, and then for another year or more in an air-conditioned room before DNA extraction.

Prey contents were determined from 102 scats. Based on previous studies (L. Emmons, personal communication; Fernandez *et al.* 1997), a dry scat diameter of 25 mm or greater was assumed to be from large carnivores (puma and jaguar) and scats <25 mm were assumed to be from small carnivores (ocelot and crab-eating fox). Results of this traditional analysis were compared with those from molecular identification. Mammalian prey identified in scats were classified as small (<1 kg), medium (1–15 kg) or large (>15 kg).

Predator species identification

To accurately assess feeding ecology, it is necessary to identify the predator species that deposited each scat. Of 70 scats with a diameter of 24 mm or more, 33 were chosen for extraction of genetic material; one possible cub scat (19.25 mm) found near a female jaguar's den was also included ($n = 34$). Scats that were mouldy, washed clean of bile by the rain, taken from latrines or suspected regurgitation were disqualified.

mtDNA was extracted from bile powder and amplified using polymerase chain reaction (PCR) methodology. The extraction method of Paxinos *et al.* (1997) using Chelex (Bio-Rad, Hercules, CA, USA) was attempted in multiple isolations, with inconsistent results. We successfully sequenced only two scat samples using this method. A variation of the Qiagen (Valencia, CA, USA) tissue protocol developed by Wasser *et al.* (1997) proved more effective. Multiple extractions were employed for all samples (Kohn *et al.* 1995). As weight per volume of scats varied, and we were trying to wash surface area, faecal material was measured by volume. Approximately 800 μ L of dried faecal material was thoroughly mixed with Qiagen loading buffer (QLB) and centrifuged at 6000 *g* for 6 min, the supernatant was then transferred to a clean tube. To minimize contamination by prey remains, the supernatant was recentrifuged and clear supernatant transferred to a new tube. This procedure was repeated until no visible debris remained at the bottom of the tube. (If necessary, more QLB was added to the faecal material and the previous procedures repeated until there was 600 μ L of supernatant.) The supernatant was transferred to a new microtube, sealed with Parafilm and incubated at 37 °C with 40 μ L proteinase K and 360 μ L ATL buffer from the Qiagen Tissue Kit. After 16–24 h a modified Qiagen Tissue Protocol was performed. After adding 400 μ L Buffer AL and 420 μ L 100% ethanol, each sample was vortexed, loaded into a Qiagen spin column, centrifuged and washed in 500 μ L Buffer AW. After centrifuging, catch tubes were emptied and the Buffer AW wash repeated. Samples were spun for an additional 2 min at 6000 *g* to dry the filters. Spin columns were then placed in a microfuge tube, and 120 μ L of AE Elution buffer, heated to 70 °C, was added. Samples were incubated at 70 °C for 5 min and spun for 1 min. The supernatant was used immediately as a template for PCR procedures and stored at –20 °C for up to 2 weeks, or at –80 °C for longer periods. Concurrent positive controls were carried out using Qiagen's Blood Protocol (1997). All isolations and PCR amplifications included positive and negative controls.

Cytochrome *b* primers were adapted from Kocher *et al.* (1989). A relatively short fragment (308 bp) was targeted initially. After these primers amplified a nontarget species in one sample we designed primers for a smaller, carnivore

specific region of 146 bp (5'-AAACTGCAGCCCCCTCAG-AATGATATTGTCCTCA-3', 5'-TATTCTTTATCTGCCTA-TACATRCACG-3'). Species diagnosis was based on 34 variable sites in a 102-bp region of this sequence. PCR reactions (50 µL) were performed with a Biometra Personal Cycler under the following conditions: 5 µL 10× buffer, 5 mM MgCl₂, 800 µM dNTPs, 0.27 µM each primer, 0.75 unit *Taq* DNA polymerase (Fisher) and 2–4 µL of template. PCR amplifications included 35 cycles (30 s at 92 °C, 45 s at 50 °C, 40 s at 72 °C); samples with visible but inadequate amounts of target sequence were amplified using 40 cycles. After amplification, some products were run on 2% agarose gels, cut out and cleaned with Spectra-Por dialysis tubing prior to filtration. We purified all amplifications with Ultrafree-MC 30 000 filters (Millipore). Single-stranded DNA-sequencing reactions were conducted with a robotic workstation (Applied Biosystems model 800) using the manufacturer's recommended conditions, and the labelled extension products were separated with an automated DNA sequencer (Applied Biosystems model 373 A) in the DNA Sequencing Core at University of Florida, Gainesville. Fragments were aligned and edited with Sequencher version 3.0 (Gene Codes Corporation).

We obtained reference sequences from blood samples of puma, jaguar and crab-eating fox at the study site. An ocelot sample was obtained from Cleveland Metropark Zoo. All reference samples are available in GenBank (accession numbers AF266472–AF266475). DNA samples that exactly matched our reference sequences were considered diagnostic in terms of species identification. Sample sequences that did not match our references exactly were compared with entries in GenBank using the BLAST program (National Center for Biotechnology Information, Bethesda, MD) to identify DNA fragments of high similarity. We used the Kimura 2-parameter model (*PAUP* version 4.0, Swofford 2000) to calculate genetic distances between DNA fragments from scats and reference sequences. A neighbour joining analysis (Saitou & Nei 1987) of cytochrome *b* sequences was used to infer species of origin. We used bootstrap resampling (1000 times), a method of testing phylogenetic groupings, to assess the robustness of species assignments.

Data analysis

Prey items found in scats are expressed as frequency of occurrence of different prey classes (number of prey class items/total number of items, excluding plants and insects) or of biomass. Biomass describes not only the absence or presence of prey, but also represents a prey type's importance in the diet in proportion to its contribution. As larger prey items are usually represented in a number of faeces, the regression equation of

Ackerman *et al.* (1984) was applied to prey weighing 2 kg or more before biomass conversion. Use of this equation assumes proportionate sampling of larger prey items. Smaller prey are likely to be represented in only one scat so biomasses were not converted. Biomass frequencies were calculated by dividing the biomass of each prey type by the total prey biomass for each carnivore species. Only those scats from which mtDNA was successfully isolated were used to compare dietary habits of predator species based on scat size and DNA. McNemar's test (Harrison 1996) was used to assess the disparity between genetic and diameter techniques.

Results

Twenty of 34 scats (59%) were successfully amplified and sequenced (Table 1), with species diagnosed from faeces up to 3 years after collection. Although a few samples contained unreadable base pairs, these were determined by running reverse sequences and resolving ambiguous sites in favour of consensus nucleotides. DNA sequences of 16 scat samples matched our reference samples exactly (100% sequence identity), and four samples varied from references by one to four base pairs (Fig. 1). Two ocelots differed at the same three bases, and one of them had an additional base-pair difference. Two samples had unresolvable regions of seven and nine base pairs, but not at diagnostic sites. Samples that were unreadable at diagnostic sites were disqualified.

Initially, we conducted genetic analysis of scats using primers that were known to work on a wide variety of vertebrates and some invertebrates (Kocher *et al.* 1989). These primers, although successful, also amplified a nontargeted species. FF22 originally clustered most closely with *Drosophila melanogaster* based on a search of available sequences using the BLAST program in GenBank; this was presumably from ingested material or, more likely, a fly caught dining on the scat. Redesigned primers, targeting a shorter sequence of 146 bp in carnivores, increased accuracy and the number of successful samples. The technical reasons for this result are straightforward: if DNA is degraded into short fragments, as is often the case in scats and other low-yield DNA sources, then a short fragment is more likely to provide an intact template for amplification (Kohn *et al.* 1995; Frantzen *et al.* 1998; Taberlet *et al.* 1999).

Of the dry-season samples, 66% (18/27) were isolated and amplified successfully. Many of the failed samples were collected during the wet season when mould may have affected DNA quality or colon cells could have washed off in heavy rains; Flagstad *et al.* (1999) actually used a water rinse to remove colon cells from scats. Only two of seven samples (28%) collected in the wet season yielded successful sequence identifications.

Table 1 Scats identified to predator using DNA sequence information. Size class change indicates where scat classification has been redetermined after DNA analysis. (Jaguar and puma are considered large carnivores; fox and ocelot are small)

Sample FF	Species	Size (mm)	Size class change	Contents
4	Jaguar	31.95		<i>Tayassu tajacu</i> (juvenile), plant
18	Jaguar	37.5		<i>Sylvilagus floridanus</i> , plant
29	Jaguar	41.2		<i>Sus scrofa</i> (bait), dicotyledon
12	Puma	30.4		<i>T. tajacu</i> (juv.), <i>Dasybus novemcinctus</i> , dicot
27	Puma	19.25	Sm > Lg	<i>T. tajacu</i> (juv.)
28	Puma	26.4		<i>Odocoileus virginianus</i> (adult), plant
63	Puma	29.35		Med. mammal (<i>Eira barbara</i> or <i>Canis familiaris</i>), plant
79	Puma	36		<i>C. familiaris</i> , plant
5	Ocelot	25	Lg > Sm	<i>Zygodontomys brevicauda</i> , <i>Marmosa</i> sp.
10	Ocelot	24.2		<i>Oryzomys</i> sp., <i>Didelphis marsupialis</i>
15	Ocelot	26	Lg > Sm	<i>Z. brevicauda</i> , reptile, crab, plant
21	Ocelot	25	Lg > Sm	<i>Z. brevicauda</i> (two individuals), monocotyledon
22	Ocelot	26.3	Lg > Sm	Muridae, iguana, bird
65	Ocelot	25.25	Lg > Sm	Muridae, lizard, monocot
68	Ocelot	27.2	Lg > Sm	Muridae, beetle, monocot
75	Ocelot	26	Lg > Sm	Muridae (two individuals), <i>Proechimys guairae</i> , bird, crab, dicot
76	Ocelot	25.6	Lg > Sm	Muridae, bird, beetle, monocot
178	Ocelot	24.9		<i>Z. brevicauda</i> (two individuals), <i>Marmosa</i> sp. (3 indiv.)
87	Fox	26.1	Lg > Sm	Muridae, fish, crab, insect
135	Fox	25.5	Lg > Sm	<i>Z. brevicauda</i> (two individuals), bird

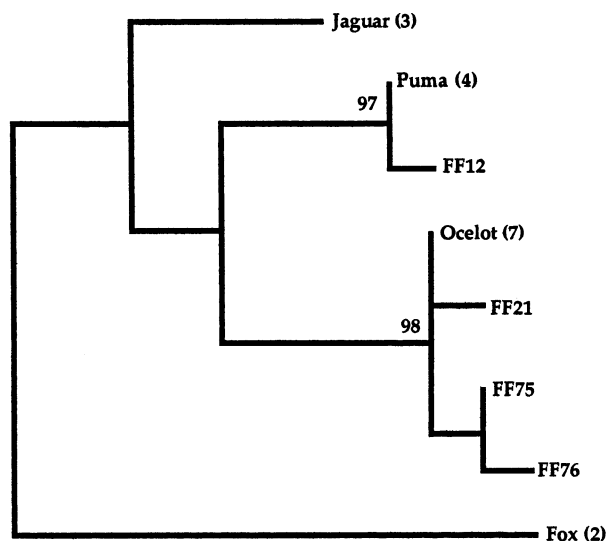


Fig. 1 Neighbour-joining tree of reference cytochrome *b* sequences and samples that were not exact sequence matches, with fox as outgroup. Bootstrap values >50%, based on 1000 replicates, are shown above relevant branches. Scat samples refer to Table 1; numbers in parentheses indicate the number of scat samples identical to reference sequences. Sequence length was too short to accurately predict systematic relationships.

Although sample sizes are small and should not necessarily be taken as indicative of actual dietary habits of these carnivores, differences between the traditional and new methods are notable (Table 2). When dietary analysis

was based on scat size with a division at 25 mm, small carnivores ($n = 3$) appeared to consume only mammalian prey, mostly <1 kg, although large prey also appeared in these scats. Analysis of large diameter scats ($n = 16$) showed evidence of prey from all categories: numerous small mammals; a fair number of medium-size mammals, mainly cottontail rabbit (*Sylvilagus floridanus*) and armadillo (*Dasybus novemcinctus*); and larger prey such as collared peccary (*Tayassu tajacu*), white-tailed deer (*Odocoileus virginianus*) and dog (*Canis familiaris*); as well as birds, crabs, fish and a few reptiles. Changing the scat size threshold to 26.5 mm (Emmons, personal communication) decreased misrepresentation of small carnivores from 10 to two, and increased misrepresentation of large carnivores from one to two. However, even this threshold indicated that small carnivores consumed large mammalian prey in two instances, a finding not supported in the mtDNA analysis. Small mammals also appeared in the large carnivore preybase, contrary to molecular findings. Using breaking points in scat size instead of DNA analysis is likely to result in misinterpretation of dietary behaviour.

Molecular analysis enabled us to transcend arbitrary size categories and calculate prey biomass frequencies for individual carnivore species (Table 3). Comparing the results from molecular techniques with those of size, we found an almost inverse dietary separation between small and large predators (Table 2). Only medium and large mammals were found in the diet of large predators ($n = 7$), and large mammals were no longer considered as small carnivore prey (Tables 1 and 2). Although FF27 was

Table 2 A comparison of prey frequencies with scats separated by size and molecular analysis

	Frequency (%) of prey types			
	Scat size		mtDNA	
	<25 mm (Small Predators)	≥25 mm (Large Predators)	Small Predators	Large Predators
Small mammals	75	46	64	—
Medium mammals	12.5	12	3	50
Large mammals	12.5	9	—	50
Reptiles	—	9	9	—
Birds	—	12	12	—
Fish	—	3	3	—
Crabs	—	9	9	—
	<i>n</i> = 3	<i>n</i> = 16	<i>n</i> = 12	<i>n</i> = 7

Table 3 Frequency (%) of prey biomass with predator scats identified using molecular analysis

	Jaguar <i>n</i> = 2	Puma <i>n</i> = 5	Ocelot <i>n</i> = 10	Fox <i>n</i> = 2
Small mammals	—	—	26	34
Medium mammals	28	45	22	—
Large mammals	72	54	—	—
Reptiles	—	—	43	—
Birds	—	—	7	23
Fish	—	—	—	31
Crabs	—	—	2	12

only 19.25 mm in diameter, molecular analysis indicated that it was from a puma that had fed on a collared peccary. Pumas also consumed white-tailed deer and medium mammals such as armadillo and dog. Two jaguar scats yielded a collared peccary and a cottontail rabbit. One jaguar scat was not included in the dietary analyses because it contained the remnants of a feral pig (*Sus scrofa*) that had been used as bait to attract jaguars for our radiotelemetry study. Molecular data transformed into biomass (Table 3) show us that reptiles were the single most important prey type for ocelots, and that foxes subsisted mainly on small mammals and fish.

When scats were divided into small (fox and ocelot) and large (puma and jaguar) predators, the diets defined by the two analyses show striking differences (Table 2). Using mtDNA, the number of prey types in the diet of small carnivores doubled. The difference between the diets of the large predators was even more notable; the main prey (small mammals) in the size analysis dropped out completely, prey types dropped from seven to two, and sample size decreased. McNemar's test (Harrison 1996) showed the difference between identification of scat donor by size and by genetic analysis to be highly significant ($\chi^2 = 7.36$,

$P < 0.01$, 1 d.f.). Small predator scats were more likely to be misclassified as large predator (83%) than vice versa (12%).

Discussion

Prey partitioning is one way in which sympatric carnivores segregate resources (Jaksic *et al.* 1981; Sunquist *et al.* 1989). Among sympatric species with similar morphology and hunting strategy, coexistence may involve the partitioning of prey, with larger predators specializing in larger animals (Rosenzweig 1966).

Although the puma and jaguar have not previously been studied concurrently, a number of studies suggest that in order to avoid competition the puma will take a wide variety of prey sizes and more small prey items where it coexists with the jaguar (Rabinowitz & Nottingham 1986; Iriarte *et al.* 1990). Jaguars select for larger prey when given a choice of prey types (Jaksic *et al.* 1981; Emmons 1991), but Emmons (1987) notes that in dense forest, where prey is small and scattered and encounters unpredictable, jaguars take whatever they find — often in proportion to availability. She hypothesized that in open grassland habitats, where water is confined to a few waterholes and large grazers are visible, prey distribution is more predictable.

Until recently it was difficult to test these theories. Although our sample size is small, results show that at Hato Piñero both large felids took large and medium prey. In contrast to dietary findings based on size analysis, fox and ocelot took prey from all categories except for large mammals, showing a wider niche breadth than the larger carnivores. With biomass data (Table 3) it is possible to identify the dietary preferences of each carnivore species, and calculate the importance of each prey type or species. Using this information, wildlife managers can calculate abundances of natural prey needed to discourage predation on domestic stock. Data from subsequent years of

this project will help us discern the degree of prey partitioning between carnivores, as well as identify livestock predators, in the llanos of Venezuela.

Scat analysis

Accurate assessment of prey requirements is essential for predicting the success of carnivores in a modified environment and in planning conservation strategies (Swank & Teer 1992). Traditional methods of identifying scats by size, shape or smell are inconsistent and unreliable; body size can vary greatly within species, and an individual animal can leave scats in a broad range of sizes. Consequently, other techniques have been attempted to discern donor species.

In a study of scats collected in the Chaco of Paraguay, Fernandez *et al.* (1997) used thin-layer chromatography of bile acids (Major *et al.* 1980) to compare the accuracy of faeces identification by size to findings using bile-acid analysis. Diameters of known puma and jaguar faeces overlapped at almost all sizes from 20 to 39 mm. Their study revealed that only 38% of jaguar and 30% of puma scats were identified correctly using the traditional method of outward physical appearance. Unfortunately, bile-acid analyses also have limitations. Taber *et al.* (1997) found a 29% error when using bile-acid assays to differentiate between puma and jaguar scats, and there is evidence that diet may affect results (Quinn & Jackman 1994).

Molecular analysis of scats also has shortcomings. Faecal DNA can be of low quantity and quality (Morin & Woodruff 1996; Taberlet *et al.* 1999), and degradation may have been a problem in our study, where field conditions were often hot and humid, making faeces prone to mould growth. While 66% of scats collected in the dry season yielded intact sequences, only 28% of samples collected in the wet season provided successful sequence identifications. One scat collected in the rainy season contained cattle hair, but was too mouldy and degraded to yield the predator's DNA. On a positive note, degraded mtDNA yields no results instead of false answers, provided contamination is carefully monitored (Foran *et al.* 1997).

Finding a large number of intact scats was a problem in this study, but a more efficient technique has been developed. Dogs have been trained to sniff out bear scats in the woods (Wasser *et al.* 1999); in 2 weeks, a team found as many faecal samples in the Rocky Mountains as we found in 11 months. This breakthrough can help design wildlife corridors by locating the well-travelled paths of rarely seen animals. For agencies with limited resources, the collection of faeces may be a useful way to survey large areas for the presence of endangered or elusive species such as felids (Foran *et al.* 1997). The only apparent negative impact of faecal analysis is that collecting all visible scat deletes markers that cats use to delineate

territories; males use scats and urine scent marks to keep track of each other, and females signal mating readiness through faecal hormones (Brown *et al.* 1994).

Diet may influence the success of molecular scatology techniques (Reed *et al.* 1997). Although prey items did not appear to amplify with our carnivore primers, predation of one carnivore on another could provide false results (Ernest *et al.* 2000). Some plant compounds are known to inhibit DNA extraction and PCR reactions (Kohn & Wayne 1997), and differential amplification of omnivore scats based on plant content could bias dietary findings both within and between species. More thorough testing for inhibitors would have improved this study, although spot checks showed that lack of DNA appeared to be the more common problem. The omnivorous crab-eating fox may have been under-represented in our study because of inhibitors, scat size thresholds (for molecular analysis) and our focus on scats containing animal remains.

Whereas mtDNA can successfully identify species (Reed *et al.* 1997), nuclear genotyping is subject to errors such as reproducibility (Gerloff *et al.* 1995), allelic dropout and false alleles (Taberlet *et al.* 1996; Kohn *et al.* 1999; Taberlet *et al.* 1999). Success rates for individual identifications typically decrease at least 20% from mtDNA success rates (Frantzen *et al.* 1998; Kohn *et al.* 1999; Ernest *et al.* 2000). Because our study did not attempt to discern individuals, it is possible that collected samples represent only a few animals, especially pumas and jaguars, which have large home ranges.

Despite the potential shortcomings, field collection methods for our study were simple and easy; samples were preserved at room temperature and transported without freezing or excess bulk, hazardous chemicals, or cumbersome permit restrictions; the international transport of faeces is not governed by the same restrictive laws that apply to transport of tissues from protected species. Scats are the only item from Appendix I species that are exempt from CITES control (Gerloff *et al.* 1995).

Summary

In much of South and Central America, the extirpation of large native prey may prompt predation on livestock (Schaller & Crawshaw 1980; Yáñez *et al.* 1986; Nowell & Jackson 1996). Sample FF29, from a jaguar, contained hair of feral pig, which had been used as bait. Sample FF79 contained remains of a domestic dog killed on the ranch. Using DNA analysis, we identified the predator as a puma, confirming the suspicions of ranch workers. These two samples indicate the potential for molecular methods as a forensic tool in dealing with predators at the interface of wild areas and agricultural lands. Of course, this technique would require local access to molecular laboratories; portable PCR analysis has been used to study

the cetacean trade (Baker & Palumbi 1994) and could be adopted for predator studies in remote areas. Field records from this study point to puma as the major culprit at Hato Piñero, responsible for up to 89% of felid predation on cattle (Farrell 1999). With more dietary evidence, it will be possible to report which species is responsible for these attacks, perhaps exonerating the jaguar, the more endangered of the two species. If problem animals can be identified, managers may be able to deal with them on an individual level, leaving the rest of the carnivore community intact. When ranchers feel more informed about the habits of these cats, corresponding persecution may be partially alleviated.

Significant aspects of the dietary habits of sympatric felids have eluded scientists for decades. Molecular techniques are finally opening a window on this component of carnivore life history, leading to a greater understanding of the total ecology of these endangered species.

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Laura Farrell's interests include behavioural ecology of felids, and finding solutions to conflicts between humans and large carnivores. The work presented here is a component of her thesis on the ecology of pumas and jaguars in the Venezuelan llanos. The field project was initiated by Mel Sunquist, whose research interests focus on large carnivore ecology and behavior. Joseph Roman is a PhD student at Harvard University, whose interests include marine ecology and conservation genetics.
