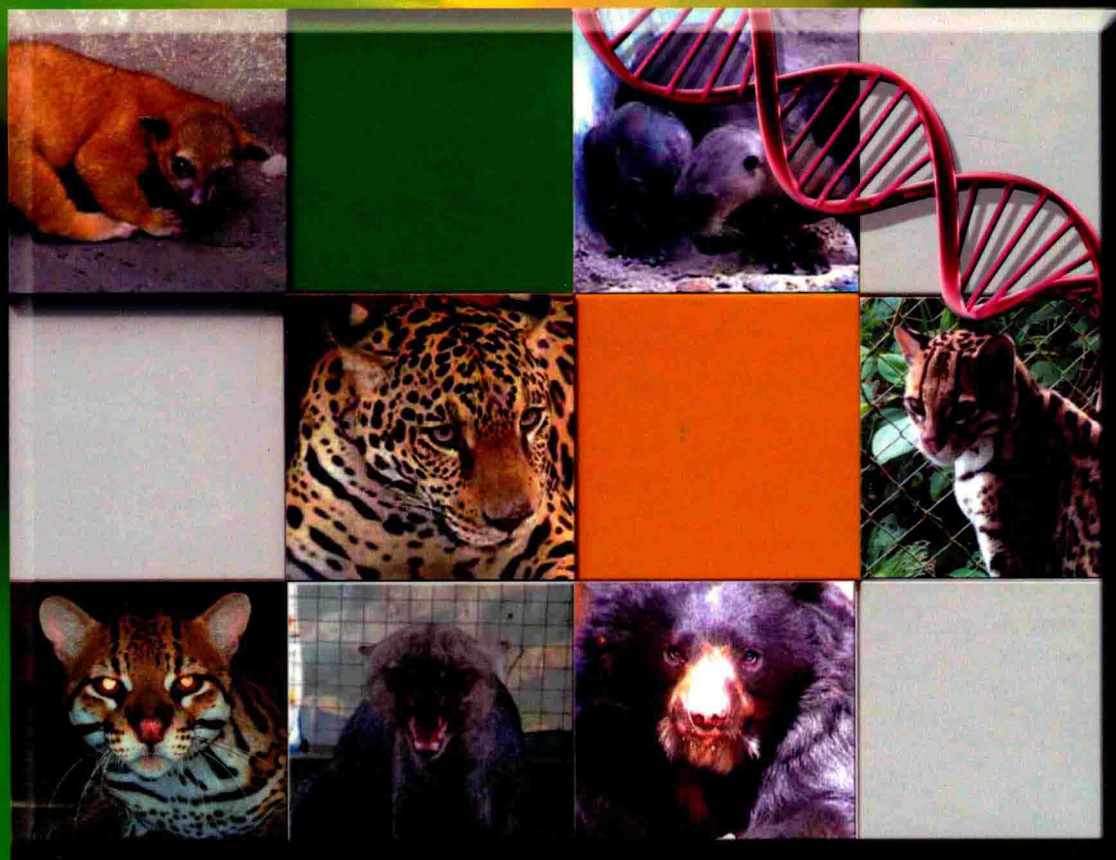


Manuel Ruiz-Garcia ♦ Joseph M. Shostell  
Editors

# Molecular Population Genetics, Evolutionary Biology and Biological Conservation of Neotropical Carnivores



*Genetics - Research and Issues*

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GENETICS - RESEARCH AND ISSUES

**MOLECULAR POPULATION GENETICS,  
EVOLUTIONARY BIOLOGY AND  
BIOLOGICAL CONSERVATION OF  
NEOTROPICAL CARNIVORES**

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**EDITORS**



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## PREFACE

The neotropical ecoregion consisting of South America, Central America, Southern Mexico, the Caribbean Islands, and Southern Florida, has long been considered an area rich in mammalian diversity and one that contains some of the world's iconic carnivores such as the Jaguar and Puma. These, and other carnivores represent the highest trophic levels within neotropical areas and as keystone species, can markedly alter omnivore and herbivore mammalian communities and indirectly, plant communities. Unfortunately, due to human population pressures, many neotropical areas and the mammals within them are increasingly at risk. This problem is compounded by the lack of current genetics, evolutionary biology and conservation data of these critical carnivores available to conservation biologists at the forefront of trying to preserve and protect these imperiled geographical areas. This book helps to meet these shortcomings by providing contributions from 60 of the world's leading scientists in the area of neotropical carnivores. The first section of the book covers molecular population genetics and phylogeography of diverse neotropical carnivores such as otters, coatis and other Mustelidae and Procyonidae, wild cats (jaguar, puma, ocelot, jaguarondi, Pampas cat, and Andean cat) and the Andean bear. Significant sections of the book are also devoted to the topics of reproduction, geometric morphometrics of wild canids and a complete paleontological view of the evolution of all neotropical carnivore groups. Furthermore, the book contains several chapters on the conservation details and varying cultural perspectives regarding the two larger and more mythical neotropical carnivores, the jaguar and the Andean bear, which together, are the paradigm for the conservation programs in Central and South America.

Chapter 1 – The Neotropics is rich in biodiversity and arguably contains some of the least understood and most understudied predators of the world. Jaguars and other carnivores represent the highest trophic levels within Neotropical areas that can markedly alter vertebrate communities and indirectly plant communities—leading to greater overall biodiversity. Their elusive nature and diffuse distributions within difficult to access areas make their data extremely difficult, time consuming and expensive to obtain. Thus, the authors considered it essential to bring together the world's leading Neotropical carnivore specialists to compile their most recent data altogether in a single publication that would be available to conservation managers of Neotropical areas.

This chapter describes the book's main themes (molecular population genetics, evolutionary biology, and biological conservation) and how it presents Neotropical carnivore data in different categories such as by guild (all Neotropical carnivores), by family, and when



appropriate, by species. The remaining part of this chapter describes specific species of interest (jaguar, jaguarundi, guigna, pampas cat, Andean mountain cat, ocelot, Andean bear, Giant Otter, sechuran fox, culpeo fox, kinkajou and the tayra) to which the authors have added significant amounts of new data and that are further discussed in succeeding chapters.

Chapter 2 – This is the first preliminary study on the molecular systematics within *Potos flavus* (Procyonidae) and in *Eira barbara* (Mustelidae). To carry out this work, 24 samples of *P. flavus*, representing three putative different populations (*megalotus*, *chapadensis* and the Western Amazon), and 68 samples of *E. barbara*, representing the five putative subspecies present in South America, were sequenced at the *mtCyt-b* gene for the first species and at the *mtCyt-b* and *mtNADH-5* genes for the second species. The main results obtained were as follows: 1- Both species showed high levels of mitochondrial gene diversity, especially *E. barbara*; 2- Within the kinkajou, the specimens representing *megalotus* and the Western Amazon populations, belong to a unique population whereas *chapadensis* in Bolivia, represented another different population. Within the tayra, only two subspecies seem to be molecularly “real” (*sinuensis*, *peruana*, *madeirensis* and *barbara* were unified in *barbara*, whereas *poliocephala* from French Guyana could be a second differentiated subspecies in South America); 3- The mitochondrial diversification process of *P. flavus* in South America seems to have occurred in the last 3 million year and even in the last 40,000 years, although the phylogenetic branch of *Potos* seems to be very old (21-24 million years ago following Koepfli et al., 2007). Contrarily, the mitochondrial diversification process in *E. barbara* was older, occurring around 7-8.2 million years ago. This could point out that the tayra diversification process was in North America or this mustelid was an “island hopper” following Simpson (1980) and migrated into South America before the complete formation of the Panamanian land bridge, 3 million years ago; 4- The different mitochondrial diversification peaks in both species were correlated with climatic changes during the Miocene, Pliocene and Pleistocene.

Chapter 3 – This is a preliminary study on the possible genetic structure and phylogeography of the Giant otter (*Pteronura brasiliensis*) in the upper Amazon basin (Colombia, Peru, Bolivia and western Brazilian Amazon) and in the Orinoco basin (Colombia) by means of sequences of the *mtCyt-b* gene. The animals from the upper Amazon and those from the Orinoco basin were not isolated and no significant heterogeneity was detected. The authors’ results showed that the animals clustered in two main clades, one only integrated by upper Amazon individuals, with moderate haplotype diversity, and the second by other upper Amazon animals as well as the Orinoco animals and one sampled in the Bolivian Amazon with a higher haplotype diversity. No population expansion processes were detected with different procedures and the Bayesian analyses determined that the two main clades diverged around 37,000 years ago, while within each one of the clades, the divergences times among haplotypes were around 10,000-20,000 years ago. These time splits were correlated with climatic changes in the fourth glacial period of the Pleistocene and during the Holocene.

Chapter 4 – Herein the authors analyzed samples of four species of the Neotropical fox genus *Pseudoalopex*, representing *Ps. culpaeus* (*Ps. culpaeus andina*, from Peru and Bolivia, and *Ps. culpaeus culpaeus*, from Chile), *Ps. sechurae* (Peru and Ecuador), *Ps. griseus* (Argentina) and *Ps. gymnocercus* (Bolivia) for 419 base pairs of the *mtCyt-b* gene. The main results obtained were as follows: 1- The ancestor of *Ps. sechurae* was the first to diverge for the taxa of *Pseudoalopex* studied around 1.1-1.2 MYA. *Ps. sechurae* was the species which

presented the highest levels of gene diversity of the *Pseudoalopex* species, probably because it is the oldest one of those studied; 2- The temporal separation of *Ps. griseus* and *Ps. culpaeus* is very recent (0.15-0.21 MYA) and no monophyly reciprocity was found in any of the analyses undertaken; 3- The divergence split between *Ps. culpaeus culpaeus* and *Ps. culpaeus andina* was around 0.17-0.22 MYA and these two *culpaeus* forms could be seen as two different ESUs in terms of biological conservation; 4- The individual of *Ps. gymnocercus* analyzed did not differentiate from the haplotypes of *culpaeus*. Two hypotheses were speculated: the taxa *gymnocercus* is not molecularly differentiated from *culpaeus* because a very extreme and recent speciation or it is an example of hybridization among two Neotropical fox species, with gene introgression of *Ps. culpaeus* within *Ps. gymnocercus*; 5- No geographical structure was found within *Ps. culpaeus andina*. This means that the populations of this species in Peru and Bolivia must be conserved as unique ESUs; 6- There was evidence of population expansion in *Ps. culpaeus* and *Ps. sechurae*, although the demographic evolution of both Neotropical foxes was different.

Chapter 5 – Herein I show new molecular data (microsatellites and mtDNA sequences) for the Andean bear based on a larger sample size (286 individuals) than previously analyzed by Ruiz-García (2003, 2007) and Ruiz-García et al., (2003, 2005). This sample was composed of individuals obtained in Venezuela, Colombia, Ecuador, Peru and Bolivia. Four main results came out of this study. 1- The evolutionary microsatellite dynamics of the markers applied to the spectacled bear revealed 20% of multiple-step mutations and an overall historical effective number of around 10,000 individuals; 2- Microsatellites detected a significant genetic heterogeneity for a large fraction of the comparisons made among the different populations considered, although this genetic differentiation was smaller than that obtained in previous studies; 3- No tests detected any significant bottleneck event in the history of the overall population nor in the spectacled bear populations of Colombia and Ecuador. In contrast, some tests detected historical population expansions in this species. This was contrasted with the possible climatic changes during the late Pleistocene. 4- The phylogeographic analysis by means of the mitochondrial control region sequences showed, in contrast to the microsatellites, little degree of differentiation among the Andean bears from Venezuela, Colombia and Ecuador. However, two Peruvian exemplars were relatively differentiated from all the other sequences analyzed. This paper discusses the integration of both sets of molecular marker results.

Chapter 6 – The authors investigate the genetic diversity and structure of guigna populations throughout their known distribution range by analyzing 1,798 bp of the mtDNA and 15 microsatellite loci in 116 individuals sampled from 32.5°S to 46.5°S in Chile and Argentina. MtDNA data reveals a moderate separation between northern and southern populations, supporting previously proposed subspecific partitions. Microsatellite data supports this north-south pattern of subdivision, showing also further structure detail revealing current demographically isolated groups. Spatial analysis of molecular variance shows a finer scale yet consistent population structure compared to the genetic assignment and clustering method. High positive correlations between genetic and geographic distances in both mtDNA and microsatellite loci suggest a consistent historical and contemporary isolation by distance pattern. The population structure uncovered by this study identifies at least five different Conservation Units for guigna populations throughout their distribution range in southern South America.



Chapter 7 – In this chapter, the authors show complementary results to the works of Cossíos et al., (2009, 2012), on the genetic structure and phylogenetics of two small Andean cats, the Pampas cat (*Leopardus pajeros*) and the Andean mountain cat (*Leopardus jacobita*). In the present study the authors increased the samples sizes to 235 individuals for *L. pajeros* and 115 individuals for *L. jacobita*, effectively making these samples the largest to date for these two species. The authors analyzed five microsatellites for *L. pajeros* and seven microsatellites for *L. jacobita* as well as the hypervariable domain 1 (*HVS-I*) of the *mtDNA* control region for both species. The main results obtained were as follows: 1- The levels of gene diversity for *L. pajeros* with microsatellites were considerable higher than in *L. jacobita* (average  $H = 0.73$  vs.  $0.42$ , respectively), with the first similar to other Neotropical felids but the second one lower than other Neotropical felids and many other Neotropical mammals analyzed from this point of view. The same was recorded for *mtDNA* sequences, with the Pampas cat ( $\pi = 0.0513$ ) presenting more than 10 times higher nucleotide diversity than the Andean mountain cat ( $\pi = 0.0047$ ). The sample which could represent the putative morphological subspecies, *L. p. budini*, was that which yielded the highest levels of gene diversity. This could mean that this is the original *L. pajeros* form from which the other forms derived. Alternatively, the northern area of Argentina, where *L. p. budini* occurs, could be a hybridization zone among several *L. pajeros* forms. 2- Microsatellite heterogeneity for the Pampas cat was significant but it was relatively low with regard to the high genetic heterogeneity found for *L. jacobita* for microsatellites. For *mtDNA*, the genetic heterogeneity was very high and similar for both species. This could indicate that for the Pampas cat the gene flow is male biased, meanwhile the Andean mountain cat populations are hardly isolated in the high land deserts of the Andes and the gene flow is more restricted for both males and females. Also this analysis puts in doubt that *L. pajeros pajeros* and *L. pajeros crucinus* are two different subspecies. Furthermore, this analysis revealed that if the different gene pools determined in *L. pajeros* are classified as different subspecies, then four different subspecies, or at least, four different evolutionary lineages must be consider in *L. jacobita*. 3- The assignation analyses presented relatively low percentages of correct assignation for *L. pajeros*, while the percentages of adequate assignation for *L. jacobita* were very high. This is related with the fact that gene flow estimates among the populations of the Pampas cat are considerably higher than for the populations of the Andean mountain cat for nuclear markers. 4- *L. pajeros* presented more evidence of population expansions during its history for microsatellites than did *L. jacobita*. For *mtDNA*, both species did not reveal traces of population expansions and *L. jacobita* showed a trend indicative of a moderate bottleneck. 5- Both species showed 4-5 % of mutations with multiple steps and different mutation rates for the microsatellites employed. 6- The effective number estimates were around 10 times higher for *L. pajeros* than for *L. jacobita* independently of the procedures employed. The effective sizes for *L. pajeros* ranged from 80,000 to 330,000 and for *L. jacobita* ranged from 12,000 to 38,000. However, these estimates seem to be higher than the current census sizes. The procedures of Hill (1981) and Pudovkin et al., (1996) were not useful for effective number estimations in this case. 7- Both species presented significant spatial structure related with isolation by distance and monotonic clinal trends, but this spatial structure was more developed in *L. jacobita*. Around 35 % of the genetic differences were explained by the geographical distances among the populations in *L. pajeros*, while around 64 % of the genetic differences were explained by geographical distances in *L. jacobita*. 8- The northern Chilean Pampas cat population seems to be an extension of the Peruvian and north Bolivian *L. p.*

*garleppi* in contradiction with García-Perea (1994), who denominated that population as a new subspecies *L. colocolo wolffsohni*. Nevertheless, more samples of that region are needed to have total clarity of what Pampas cat is living there. Additionally, in Bolivia, the authors determined the existence, at least, of two putative subspecies (*garleppi* and *steinbachi*). Finally, although molecular conclusive studies are needed, the first molecular studies indicate that the existence of a unique Pampas cat species is more probably than three different species such as García-Perea (1994) proposed.

Chapter 8 – A total of 44 wild jaguarundis were sampled throughout Mexico, Guatemala, Costa Rica, Colombia, Venezuela, Ecuador, Peru, Bolivia and Brazil and sequenced for three mitochondrial genes (*ATP8*, *16S rRNA*, *NADH5*). This is the first molecular population genetics and phylogenetic study of this species and the most relevant results were as follows: 1- The gene diversity levels for the jaguarundi at the three mitochondrial genes sequenced were very elevated as it was found for other Neotropical wild cats such as the jaguar, ocelot, margay and the Pampas cat; 2- The levels of gene heterogeneity among putative subspecies or among countries was extremely small, although this species has a broad distribution from southern USA to Argentina; 3- Additionally, the phylogenetics trees (genetic distances, maximum likelihood, maximum parsimony and Bayesian) showed that no molecular subspecies were defined in contradiction with the morphological classifications of Allen (1919), Cabrera (1957) and de Oliveira (1998); 4- Bayesian and network procedures showed that the first haplotype divergence process in the jaguarundi began around 2.0-1.6 MYA, with a second haplotype divergence event around 1.1-0.8 MYA, followed by other haplotype splits around 0.75-0.5 MYA, 0.34-0.32 MYA, and 0.16-0.11 MYA as well as many haplotype divergence events in the last 30,000 YA. These haplotype process splits were correlated with climatic changes during the Pleistocene; 5- Some evidence of population expansion was determined for the jaguarundi around 400,000 YA, especially for the *ATP8* marker, and a slightly higher population declination was detected for the last 20,000 YA for *ATP8* and *16S rRNA* loci.

Chapter 9 – Several taxonomic classifications have been proposed for the ocelot, but almost all of them were based on non-molecular genetics studies. Herein, the authors analyzed 294 ocelots from Guatemala, Costa Rica, Colombia, Venezuela, French Guiana, Ecuador, Peru, Bolivia, Brazil and Paraguay for 10 microsatellite loci as well as 118 skulls for biometrics analyses. The authors' genetics and craniometrical data results did not support the three classificatory schemes the authors analyzed and tested (Allen, 1919; Murray and Gardner, 1997; Eizirik et al., 1998). It seems clear that the *albescens* form from Southern Texas and northern Mexico is a defined subspecies as is *pardalis* in Central America. However, their molecular analyses did not determine important levels of genetic heterogeneity among a large fraction of the putative ocelot subspecies in South America. Therefore, previously defined subspecies such as *aequatorialis*, *pseudopardalis*, *melanura* and *steinbachi* could be assigned to a unique subspecies, *pseudopardalis*. In contrast, the craniometric analysis differentiated *steinbachi* from the other South America putative ocelot subspecies. This was mostly likely due to the smaller skull size of the *steinbachi* individuals analyzed. It's possible that the southern South America form, *mitis* could belong to the *aequatorialis*, *pseudopardalis*, *melanura* and *steinbachi* group. If so, then this group should be defined as *mitis*. Additional genetics and morphometric studies are especially needed to determine the taxonomic status of *pusaea*, *mitis*, *nelsoni* and *sonoriensis*.

Chapter 10 – The authors analyzed for 12 nuclear DNA microsatellites in 4 wild cat species (European wild cat, ocelot, puma, and jaguar) representing four different phylogenetics felid lineages. The objective of the authors' study, using these species and molecular markers, was to obtain more data about the molecular evolution of microsatellites. The main findings of this study are: 1- From the measurements of diverse genetics variables and statistics in the four species, the authors determined that the ocelot showed the highest number of alleles, number of repeats, allele range and levels of heterozygosity. However, no significant differences were observed among the average microsatellite mutation rates observed in the four species of felids studied. 2- The authors estimated two independent average mutation rates ( $3.116 \times 10^{-5}$  and  $5.353 \times 10^{-5}$ ) using two different phylogenetics strategies. However, there was no significant difference between these two estimates. 3- The authors found the observed mutation model to be basically a uni-step mutation model or a two-phase mutation model. The four felid species showed an average stepwise mutation model for 92-94 % of the uni-step mutations. 4- The regression models the authors applied among different genetic diversity statistics, samples sizes and other variables showed: a- the allele range was clearly more correlated with the allele number at the microsatellites studied than to the allele dispersion, b- There was no clear relationship between the microsatellite sizes and the degree of genetic variability that these microsatellites showed in the four felids studied, c- There was no evidence of a positive relationship between more mutations and an increase in microsatellite size in the authors' study. This finding was independent of the microsatellite size being measured by its total size or by the number of repetition tandems, d- There was no relationship between the allele expansion rate and the level of genetic diversity determined in these microsatellites, e- With the exception of the ocelot, the other three the authors' analysis of felid species individually, as well as the overall analysis of the four species together, did not detect an average winning or losing of repeat tandem numbers regarding the employed microsatellites cloned in the domestic cat; therefore, ascertainment bias was not found in this study, f- Sample size played an important role in determining the accurate levels of gene diversity in the four felid species studied. The authors determined the number of alleles per locus to be around 42-50 %, the heterozygosity to be around 23-28 % and the  $\theta$  statistic for multiple mutation models to be around 10-13 %, per sample size. The number of alleles per locus, was the statistic most influenced by sample size whereas  $\theta$  was the statistic least influenced by the sample size. 5- There was a significant fraction of microsatellites affected by mutation bias by using the Garza et al., (1995)'s procedure and 6 – In contrast to many authors who have suggested that microsatellite markers are not useful as phylogenetics tools, the authors document that, with certain restrictions and considerations, some microsatellite sets can be helpful in phylogenetics tasks, at least, in the felids.

Chapter 11 – A total of 250 jaguars directly sampled in the wild (Guatemala, Costa Rica, Colombia, Venezuela, French Guiana, Peru, Bolivia and central and western Brazilian Amazon) were analyzed for 12 DNA microsatellite loci and for three mitochondrial genes (*NADH5*, *16S rRNA* and *ATP8*). The main results were as follows: 1- The levels of gene diversity were very high for microsatellites as well as for mt markers. These levels were higher than those obtained in other studies by Eizirik's team. Explanations of why this occurred are herein discussed. 2- The highest gene diversity levels were found for the western Amazon areas for microsatellites as well as mt markers, with lower gene diversity levels for areas far as away as central and eastern Brazil and Central America. 3- The levels of genetic heterogeneity were small for the samples classified by morphological subspecies, by countries

and by considering the Amazon River as a barrier. Therefore, there is no clear evidence of the existence of “real” subspecies in the jaguars, especially, for the forms of South America. It was also clear that the Amazon River was not a geographical barrier for this large species, disagreeing with the claims of Eizirik et al., (2001). The levels of genetic heterogeneity by country were slightly higher than by subspecies. This could have interesting repercussions in the conservation politics of each Neotropical nation where jaguars live. Several AMOVAs showed that the majority of gene diversity was placed in individuals and that no other upper hierarchical clusters have significant importance. The theoretical gene flow estimates were very high for microsatellites as well as mt markers. However, the mt DNA gene flow estimates were higher than for the microsatellites, disagreeing with the results of Eizirik et al., (2001). 4- The assignment analyses with microsatellites as well as the spatial tree analyses with mt DNA markers showed no significant geographical clusters for the jaguars analyzed. Even the percentage of first generation migration jaguars was elevated (10-20 %) showing the importance of gene flow in this species and, possibly, the non-existence of putative subspecies. 5- The overall jaguar sample analyzed at the mt *NADH5* locus showed a very significant population expansion from the western Amazon in three different periods (500,000-600,000 YA; 150,000-250,000 YA and 10,000-55,000 YA). The climatologic changes in these periods are discussed in relationship with the jaguar population expansions detected in this work.

Chapter 12 – Forty one jaguar skulls from Colombia were measured for 46 quantitative morphometric variables. The authors detected no differences between two supposed subspecies of jaguars or their gender. However, size was more important in determining individual differences than shape. Therefore, morphometric data seem to be less powerful in detecting differences among different gene pools than DNA microsatellites or other molecular markers.

Chapter 13 – A firm understanding of the reproductive biology of threatened species is critical for the promotion of effective conservation strategies. The authors review the reproductive characteristics of the ~65 species of Neotropical carnivores, including male and female anatomy, mating systems, estrus cycles and induced ovulation, delayed implantation, placentation, gestation, parturition, and lactation. This includes the compilation of a variety of quantitative and qualitative reproductive traits from various sources, such as litter size, individual mass at birth, and length of gestation and weaning periods. Also, the authors discuss the use of contraception in captive Neotropical carnivores and its association with the risk of cancer in jaguars. In addition, the authors identify gaps in the knowledge of life history in specific Neotropical carnivore species that should become priorities for further conservation efforts.

Chapter 14 – Terrestrial placental carnivores (Mammalia, Carnivora) of South America are recorded as being in existence since the late Miocene (Huayquerian), with representatives of the families Felidae, Canidae, Ursidae, Mustelidae and Procyonidae. The arrival of eutherian carnivores to South America is closely associated to the rising of the Panamian Isthmus that permitted the biogeographic event called the “Great American Biotic Exchange”. In this chapter the authors update the latest advances in the systematics, phylogeny, biostratigraphy, biogeography and paleoecology of South American land carnivores. The first records correspond to procyonids dated as late Miocene (Huayquerian). At the end of the Pliocene (Vorohueian) canids (Caninae) and mustelids (Mustelinae) appear, but it is at the beginning of the Ensenadan (late Pliocene – middle Pleistocene) when the group diversified,



represented by the first record of Ursidae, Felidae, Mephitidae, Lutrinae and large canids. The diversity of fossil and recent carnivores is a consequence of several independent immigrations (also within subfamilies and genera), and the diversification of these immigrants in South America.

Chapter 15 – The home ranges and core areas of five female and four male Andean bears (*Tremarctos ornatus*) inhabiting the Intag region in Ecuador were estimated from a total of 1,349 telemetry locations for females and 412 for males between September 2001 and December 2006. Multi-annual and seasonal home ranges were estimated using fixed kernel 95% analysis, and multi-annual and seasonal core areas were estimated using fixed kernel 50% analysis.

Home ranges and core areas were both several times larger for males than for females. Core areas suggested differences in structure between males and females, with females mostly having just one principal core area while most male core areas had multiple nuclei of roughly equal sizes.

This study found no evidence of territorial behavior. All the bears in this study showed some degree of core area overlap, suggesting intraspecific tolerance for the species. Annual core area overlap was lower between males than between females, with male over female overlap higher than female over male.

Seasonally, core area overlap between females, male to female and female to male were all higher in the dry season (which mostly coincides with the maize season) than in the wet season. However, male-male core area overlap was considerably lower in the dry season than in the wet season.

Chapter 16 – Hematologic and chemical blood values are baseline parameters to evaluate the health status of a given captive or wild population. These parameters can also measure physiological responses in the face of intrinsic or environmental stress produced by natural or human interventions. Nevertheless, this is only achieved by comparing with the normal values of the species. Various molecular studies on the Ecuadorian Andean bear (*Tremarctos ornatus*) populations have revealed that the homozygous levels are high for hypervariable microsatellite markers and that effective numbers are strongly limited. In order to complement ecological and genetic studies, the physiological traits of this species were studied. Eight hematologic traits and 10 biochemical variables were measured in two Andean bear groups, one comprised of captive animals in zoos and “centros de rescate” and the second comprised of individuals assigned to a rehabilitation program. Additionally, the hematologic and biochemical variables were compared to those obtained from three wild bears. The two main aims developed in the present study were to analyze if Castellanos’ rehabilitation procedure affects in these hematologic and biochemical traits regarding those values found in captive zoo animals. If so, in what sense and magnitude were these differences developed? Results show that the hematologic variables presented higher trends in favor of differences among the rehabilitated-free group relative to the captive group (three out of eight) than did biochemical variables (one out of ten).

Chapter 17 – The Andean bear or spectacled bear (*Tremarctos ornatus*), is widely distributed along the flanks of the Andes in South America. It is an endemic species to the tropical Andes. In Bolivia it is present in the departments of La Paz, Cochabamba, Chuquisaca, Santa Cruz, Beni and Tarija. The conservation status of the Andean bear has been evaluated during recent years, and these studies have identified important strongholds for bear conservation as well as areas where threats may affect the viability of wild

populations. Because there is currently no explicit legal protection for this species in Bolivia, the only legal protection afforded is within protected areas. This chapter includes information on conservation status, aspects related to geographic distribution, behavior, ecology, population size, threats and possible means of protection.

Chapter 18 – As large predators, jaguars (*Panthera onca*) require vast expanses of well conserved land, abundant prey and few people. This study reviews three different ecological studies on jaguars living in unprotected lands. The first study focuses on Colombian jaguars living with indigenous peoples in Amazonia, while the second study examines a Colombian jaguar population living in cattle ranches persecuted for depredation. The third study concerns jaguars surviving in the Rupununi savannahs of Guyana, where cattle ranching is withering and tourism is gaining ground. All examples have five main common factors that enable jaguars to survive in unprotected lands: low human density, poor soils, inaccessibility, wild prey availability and closeness to large protected areas ( $> 3,000 \text{ km}^2$ ). The authors propose that the long-term conservation of jaguars will depend on conserving populations in unprotected lands as a complement to protected areas.

Chapter 19 – The jaguar (*Panthera onca*) is the largest cat in the New World and faces threats including direct persecution, habitat loss, and decimation of prey populations. Typically, conservation approaches focus on individual sites and do not account for larger landscape dynamics over the range of the jaguar. Furthermore, conservation programs tend to remain internal to the organization in which they were born. However, expanding beyond this insular approach to jaguar conservation can have much broader impacts and result in lasting conservation programs. The authors present a range-wide strategy for jaguar conservation, seeking general acceptance and use by the conservation community. Working together on a single, range-wide framework allows greater opportunity to advance jaguar conservation. The authors' strategy, the Jaguar Corridor Initiative (JCI), is built upon previous range-wide priority setting exercises that identified core jaguar populations. In this chapter, the authors explain how they incorporated corridors connecting these populations to allow for jaguar dispersal and genetic exchange, thereby adding a critical element to the long-term survival of this species. Then they describe how they are assessing the jaguar populations and corridors in the field. These empirical data provide further scientific backing to the areas identified in the conservation network, allow for refinement, and give a baseline from which monitoring can occur. Finally, the authors describe their conservation efforts across the JCI. The large size of the JCI necessitates working at all levels of engagement, from the national level to the local landowner. Furthermore, each site in the JCI faces different challenges, so varying conservation approaches must be used across jaguar range to result in lasting conservation success. The authors provide examples of conservation efforts with the hope that other biologists and conservation practitioners across jaguar range will embrace the JCI and build off their beginnings. The authors have an opportunity to ensure an enduring future for jaguars by preemptively preventing fragmentation, thereby maintaining connected populations and allowing the biology and ecology of the jaguar to be preserved. This can only be accomplished through collaborative and transparent approaches across the range of this species.

Chapter 20 – Carnivores are usually found in low population densities, often have relatively wide ranging movement patterns and as such, require large areas to ensure their conservation. The first two levels of information required for making and assessing conservation decisions for carnivores at a national scale are the diversity and distribution of



species present. Between 2006-2011 the authors systematized 7,731 distribution records across Bolivia dating from 1902 to present for 27 confirmed carnivore species in six families and 19 genera, which resulted in 6,729 records with sufficient geographic and taxonomic confidence with which to develop updated distribution maps and limits for each species. The number of confident distribution records per species varied from 5 to 1,659 records (mean = 249 records). In order to assess the spatial distribution of total carnivore distribution records the authors analyzed the data as a function of the nine Departments and 22 national protected areas of Bolivia, as well as 100 km<sup>2</sup> and 10,000 km<sup>2</sup> countrywide grids. La Paz Department, and especially the protected areas of northern La Paz, had the greatest concentration of carnivore distribution records, whereas Oruro, Pando and especially Chuquisaca departments had the lowest number and density of carnivore records. All 27 confirmed carnivore species had confident records in at least one national protected area and projected distributions suggest that all carnivore species will eventually be registered in at least five national protected areas. Based on continental distribution patterns 5 additional carnivore species may eventually be registered in Bolivia. The authors discuss these findings and highlight the conservation implications.

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