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Research and Conservation Priorities for Tortoises and Freshwater Turtles of Colombia

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Abstract

The objective of our study was to review and quantify the level of knowledge of the biology of tortoise and freshwater turtle species of Colombia based on studies conducted in the country. We used the resulting rankings in knowledge, in combination with IUCN threat category, presence in protected areas, and endemism, to propose conservation priorities. This process also allowed us to evaluate which aspects of turtle biology have been least studied. Four species obtained total values of zero or one over the 21 knowledge criteria employed, so they were ranked as the highest priority for research based on the lack of knowledge of their biology: Black-lined Toad-headed Turtle (*Mesoclemmys raniceps*), Amazon Toad-headed Turtle (*Mesoclemmys heliostemma*), Gibba Toad-headed Turtle (*Mesoclemmys gibba*), and Dunn's Mud Turtle (*Kinosternon dunni*). Moreover, species in the family Chelidae in general were found to have limited levels of knowledge, which makes this group a priority for investigation. Evaluation of the distinct criteria used in the knowledge assessment revealed that the best-known criteria were geographic distribution (modeled), presence or absence in protected areas, and clutch size. The most poorly known biological characteristics, which constitute research priorities, are the frequency of nesting, longevity and generation time, and population parameters. According to the criteria used, the priority species for conservation were the Magdalena River Turtle (*Podocnemis lewyana*), Dahl's Toad-headed Turtle (*Mesoclemmys dahli*), *K. dunni*, and Maracaibo Wood Turtle (*Rhinoclemmys diademata*), three of which are endemic or semiendemic (*R. diademata* only occurs in Colombia and Venezuela), followed by two species of *Mesoclemmys*.

Keywords

testudines, knowledge, threats, South America

Introduction

With 27 species of freshwater and terrestrial turtles (continental turtles), Colombia is considered the seventh most species-rich country in the world and second at the level of South America behind Brazil (Turtle Taxonomy Working Group, 2014). Nine families of turtles occur in Colombia, which makes it the country with the greatest number of turtle families (Asociación Colombiana de Herpetología, 2011; Páez, Morales-Betancourt, Lasso, Castaño-Mora, & Bock, 2012a). Despite this great diversity, turtles are far from being one of the best-studied animal groups in Colombia and many aspects of their basic biology remain unknown (Páez et al., 2012a). The first data on Colombian turtles dates back to the beginning of the 19th century when Jesuit missionaries and foreign chroniclers anecdotally described the natural history and habits of these animals, and the uses that human

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communities made of them (Coutinho, 1868; Humboldt & Bonpland, 1826a, 1826b; Medem, 1968). Federico Medem was the first to conduct rigorous studies on freshwater turtles in Colombia beginning in the middle of the last century. In addition to his contributions in terms of articles, book chapters, and other publications (Anonymous, 1986), Medem inspired a generation of Colombian researchers who followed in his path. The availability of scientific information on this taxonomic group has grown significantly, with the publication of the first and second editions of the Red Book of Colombian Reptiles (Castaño-Mora, 2002; Morales-Betancourt, Lasso, Páez, & Bock, 2015a), some key documents targeting strategies at the national level (Ministerio del Medio Ambiente, 2002; Morales-Betancourt, Páez, & Lasso, 2015b), the book by Páez et al. (2012a), and the various publications of biologists working on turtles in Colombia.

In terms of conservation, Medem again was one of the first to call attention to the status of populations of some species of continental turtles in Colombia and to publish information on the need for implementing conservation policies (Ministerio del Medio Ambiente, 2002). On the other hand, the first comprehensive summary of the information available on the turtle species of Colombia (Castaño-Mora, 1992) identified multiple knowledge gaps and threats to various species in the country, stimulating the initiation of research and conservation projects on different species. Colombia is no stranger to the global problems that affect the viability of turtle populations. In 2002, the Red Book of Colombian Reptiles reported that 12 of the continental species were threatened. Three species were Critically Endangered (Red-footed Tortoise: *Chelonoidis carbonarius*, Giant South American River Turtle: *Podocnemis expansa*, and Yellow-spotted River Turtle: *Podocnemis unifilis*), three Endangered (Yellow-footed Tortoise: *Chelonoidis denticulatus, M. dahli* and *P. lewyana*), and six Vulnerable (Red Side-necked Turtle: *Rhinemys rufipes*, *R. diademata*, Colombian Slider: *Trachemys callirostris*, *K. dunni*, White-throated Mud Turtle: *Kinosternon scorpioides albogulare*, and Red-headed Amazon River Turtle: *Podocnemis erythrocephala*). Additionally, five species were considered Near Threatened and the remaining four were categorized as Data Deficient (Castaño-Mora, 2002); 13 years later, using the most recent IUCN (2012) criteria, the second Red Book of Colombian Reptiles (Morales-Betancourt et al., 2015a) reported changes in both the percentage of threatened species, as well as in the specific categories assigned to different species. In this analysis, 10 of the continental turtles were categorized into one of the three categories of threat. The slight decline in the percentage of threatened species in the two books does not indicate that threats have ceased or that conditions for populations of these species have improved; rather, it is due to differences in the application of the criteria during the two exercises, and the availability of new information that permitted updated categorizations.

To identify specific conservation actions that will be effective, it will be necessary to understand the state of knowledge and conservation status of each species. Conservation status normally is based on criteria proposed by the IUCN, which take into account factors such as the number of populations remaining, the size of the current geographic distribution, and information on latent threats (IUCN, 2012). Nevertheless, other methods have been used when the minimum data required by the IUCN for a status assessment do not exist. For example, the Environmental Vulnerability Score is often used when data on populations are lacking. This method is based on a combination of information about geographic distribution, use of different habitats, and other specific characteristics that vary according to the taxon being evaluated, such as reproductive specialization or response to anthropogenic perturbation (e.g., Wilson, Mata-Silva, & Johnson, 2013).

In terms of assessments of the state of knowledge of a species, quantitative analyses have been complex undertakings (Alavi & Leidner, 2001; Carter, 1998; Housel & Bell, 2001). Nevertheless, the majority of methods employed have attempted to identify gaps in existing information (Lovich & Ennen, 2013) based on the number of publications available for each species or number of publications that focus on specific topics for each species (Lovich & Ennen, 2013; Stevenson, Guzmán, & Defler, 2010).

For the continental turtles of Colombia, the available information on each species summarized in the book "Biología y Conservación de Tortugas Continentales de Colombia" was the basis for a preliminary, nonquantitative analysis of some information gaps (Páez et al., 2012a). In that review, population biology and reproduction were identified as areas with scarce information for the majority of species. For example, almost none of the Colombian species have basic population monitoring data to indicate whether conservation measures that have been undertaken have had any real impact on these populations.

This article has three objectives related to the need to define priorities for research and conservation for Colombian continental turtles. First, to establish the state of knowledge for the continental turtles of Colombia based on the existence of information compiled on specific aspects of their biology and natural history. Second, to propose conservation priorities from the categories established by the IUCN, taking into consideration additional factors such as the presence of a species in protected areas and its extent of endemism. Third, to identify priority research topics, not only in order to increase our knowledge of the species but also to permit the formulation of more rigorous conservation strategies for them.

Methods

To identify research priorities for Colombian continental turtles, we scored each of the 27 species according to the published level of knowledge on their biology and threat status. We used 21 criteria that cover basic information on distribution, demographics, natural history, habitat, threats, phylogenetic rarity, evolutionarily significant units (ESUs), independent management units (MUs), genetic diversity, and molecular ecology (Table 1). The last four criteria were based on data from studies using molecular tools. Each criterion received a binary code, assigning a value of one if there was at least one published study related to the criterion, or a value of zero if there were no studies on the topic. Subsequently, we calculated the total for each species as the sum of the binary scores. The only sources of information we considered as valid were scientific articles, published books, and book chapters, as well as pre- or postgraduate theses deposited in university libraries. The primary sources of information were the species accounts published in the book "Biología y Conservación de Tortugas Continentales de Colombia" (Páez et al., 2012a). However, we also included subsequently published studies or other older studies that were not mentioned in the book.

Under this scoring system, the species with the lower scores would be higher priorities for research, since their state of knowledge is limited. In a complementary analysis, we also included factors such as the threat level and degree of endemism, considerations relevant to prioritize research, given that endemic and endangered species require data for directing the development of management strategies. A species was penalized using these complementary criteria if it was not endemic or not threatened, decreasing its research priority ranking.

Usually, assessments of conservation priorities include criteria of threat level, representation in protected areas (protection level), and irreplaceability (*uniqueness*; Brooks et al., 2006). We combined four criteria to determine conservation priorities for Colombia's continental turtles: (a) the IUCN threat category according to the Red Book of the Reptiles of Colombia (Morales-Betancourt et al., 2015a; CR = 1, EN = 2, VU = 4, Data Deficient [DD] = 4, NT = 5, others = 6), (b) endemism (endemic to Colombia = 1, not endemic = 6), (c) occurrence in protected areas (populations in PAs = 6, without populations in PAs = 0), and (d) research priority (0–6) as previously established. We assigned different weights to each criterion to obtain the final conservation priority value, arguing that the degree of threat is the most important factor (0.4), followed by endemism (0.3), the protection level (0.2), and finally level of research priority (0.1). The latter criterion was included in the analysis, given that if a species is poorly known (a high research priority), it should have priority for conservation due to the precautionary principle. In addition, we evaluated the level of knowledge for each criterion by summing the number of species for which information for that criterion was known. On the basis of this, we discuss the major knowledge gaps for continental turtles in Colombia and identify research areas that need to be addressed urgently.

Results

Our literature review permitted us to quantify the state of knowledge of the continental turtles of Colombia. The average level of knowledge was 5.6 out of 21 criteria evaluated ($SD = 3.95$), and no species had information for all criteria (Figure 1). Two species, *M. raniceps* and *M. heliostemma*, had no information for any of the criteria. According to the scoring system used, these are thus the species of greatest research priority for the country, followed by *M. gibba*, *K. dunni*, and *R. rufipes* (Figure 1). The three best-known species, and therefore lesser priorities for research, were *P. lewyana*, Chocoan River Turtle: *Rhinoclemmys nasuta*, and *T. callirostris* (Figure 1). Four of the five species of highest priority for research belong to the family Chelidae. By including threat and endemism criteria in prioritizing research needs, our priority rankings would change slightly, making the five species of highest priority *K. dunni*, *M. raniceps, M. heliostemma*, *M. dahli*, and *R. diademata*. The species *K. dunni* moves up in this priority list because of its endemism and threat level.

The results for the analysis of conservation priorities were slightly different. According to the criteria used, the highest priority species for conservation in Colombia are *P. lewyana*, *M. dahli*, *K. dunni*, *M. raniceps*, and *M. heliostemma* (Figure 2). The latter two species were listed as priorities because their threat category is DD, and they are the least known. The category DD was assigned a value equal to the category Vulnerable (V) in this analysis, again invoking the precautionary principle. The three highest priority species for conservation were the only three endemic species of Colombia, all of which are included in some IUCN threat category (Morales-Betancourt et al., 2015a).

Assessment of the overall level of knowledge of the different criteria showed that the best-known aspects concerning continental turtles are their geographical distribution (derived from models), presence or absence in protected areas, and clutch size. On the other hand, only one species had information about longevity or generation time, while in general, population parameters such as population dynamics and survival rates are also were poorly known (Figure 3).

Discussion

The results of this analysis indicate that there are still significant gaps in biological information for the majority

Table 1. Criteria Used for the Classification of the Level of Knowledge of the Continental Turtles of Colombia.

Criterion	Definition
Geographic distribution	Quantitative models of geographic distribution (area of occupancy, extent of presence, or statistical models).
Population estimates	Measures of density or abundance estimated with statistical methods (mark-recapture, distance methods, etc.).
Abundance (index)	Estimate of relative abundance (indices, catch per unit effort).
Home range	Estimate of home range area (radiotelemetry, mark-recapture, thread-tracking, etc.).
Habitat (quantified)	Quantitative evaluation (not descriptive) of the habitat (use, preference, etc.).
Population dynamics	Studies of more than 1 year evaluating population parameters and sizes.
Growth	Studies on growth of the species (in situ).
Size or age of sexual maturity	Representative field studies on size or age of sexual maturity.
Longevity, generation time	Field studies that evaluate the longevity and mean time between two consecutive generations.
Sex determination	The mechanism of sex determination is known for the species (not restricted to Colombian populations).
Number of clutches per season	Studies that determine the number of clutches or nests per female per reproductive season, or year if it is continuous (not restricted to Colombian populations).
Clutch size	Field studies on average clutch size.
Interannual nesting frequency	Field studies that evaluate whether or not a female lays eggs every year, or with what frequency they nest (annual, biannual, etc.; not restricted to Colombian populations).
Survival rate	Mark-recapture studies over multiple seasons or sites that evaluate the survivorship of different age, sex, or size classes.
Presence in protected areas	The presence of the species is known within some national-level protected area (PNN in Colombia).
Effect of anthropogenic activities	Studies that have specifically evaluated the impact of a human activity on some population of a species (impact of hunting, metal contamination, etc.).
Studies ex situ	Studies on the biology or behavior of a species in captivity.
Phylogenetic rarity	Studies that determine the phylogenetic uniqueness or distinctiveness for a species that occurs in Colombia (e.g., phylogenetic studies).
ESU	Studies that determine ESUs for a species that occurs in Colombia (e.g., phylogenetic and phylogeographic studies).
MU	Studies that determine MUs for a species that occurs in Colombia (phylogenetic or population genetic studies).
Genetic diversity and molecular ecology	Studies that evaluate genetic diversity using molecular tools in order to examine demographic or ecological information, such as multiple paternity, natal philopatry, population expansion, bottlenecks, genetic drift at different spatiotemporal scales, for a species that occurs in Colombia (i.e., studies of phylogeny, phylogeography, population genetics, and molecular ecology).

Note. ESU = evolutionarily significant units; MU = management units.

of Colombia's continental turtles, despite the efforts to advance the understanding of their biology since the publications of Federico Medem in the 1950s to 1980s. Moreover, these deficiencies are not homogeneous across species or among the knowledge criteria evaluated. The collective state of knowledge analysis showed that most of the published studies have concentrated on a few species, such as *P. lewyana*, *R. nasuta*, *T. callirostris*, and *P. expansa* (Bock, Páez, & Daza, 2012; Carr, Giraldo, & Garcés-Restrepo, 2012; Giraldo, Garcés-Restrepo, & Carr, 2012a; Morales-Betancourt et al., 2015a; Páez, Restrepo Isaza, Vargas-Ramírez, Bock, & Gallego-García, 2012b), while for other species or genera, the lack of even the most basic information is almost complete. This is the case with *M. raniceps*, *M. heliostemma*, *M. gibba, K. dunni, R. rufipes*, and *R. diademata* (Forero-Medina et al., 2012b; Morales-Betancourt et al., 2015a; Morales-Betancourt & Lasso, 2012a, 2012b, 2012c, 2012d; Morales-Betancourt, Lasso, & Páez, 2012a). Possible reasons for these biases are as much of biological origin as due to pragmatic and economic considerations. Usually, researchers prefer to study species with a greater probability of being detected that occur in more accessible locations, or that face conservation problems due to

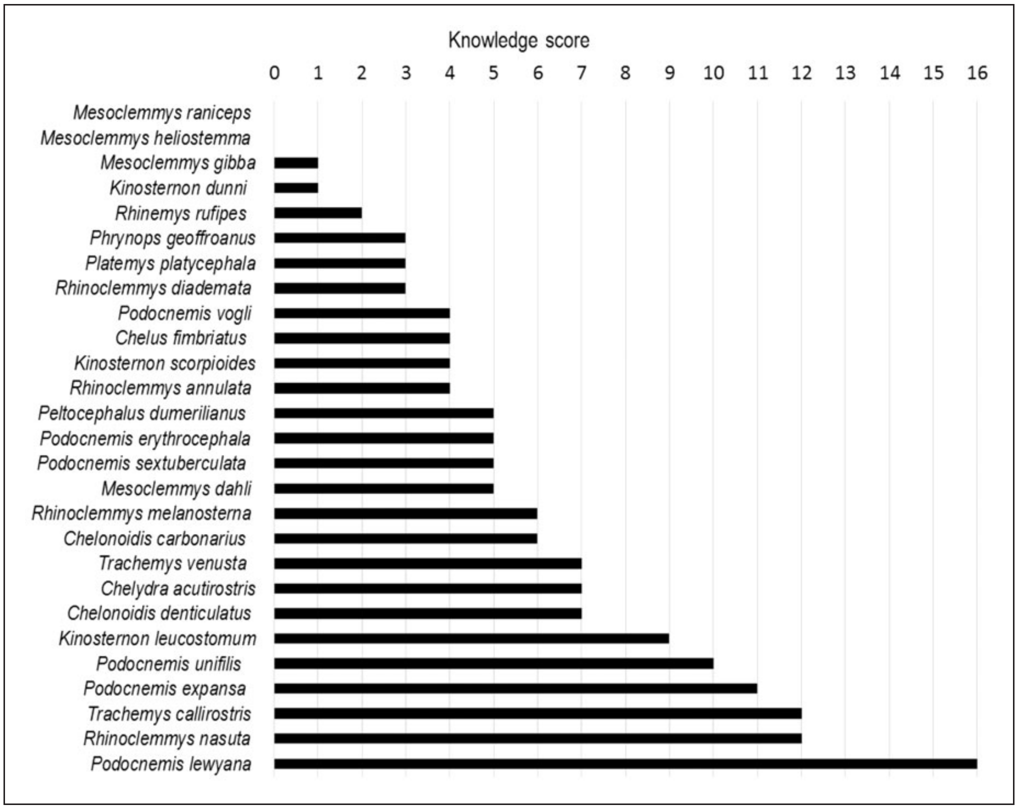

Figure 1. Classification of the species of continental turtles of Colombia by priority for research, considering only knowledge (lower values imply a greater priority; the maximum value is 21).

their economic value to humans. For example, the case of most species of the genus *Podocnemis* and the species *T. callirostris*, due to their levels of exploitation generating conservation concerns. In contrast, a common factor shared by the least studied species (many of the family Chelidae, which paradoxically has the greatest species richness in the country) is the difficulty of access to the sites where they live, their apparent low densities or difficulty in detecting their presence, and the lack of research groups working in the vicinity of their populations.

Clearly, there are not only biases at the taxonomic level, but there also are large gaps in knowledge available on biological aspects of various species that greatly affect the planning and execution of concrete actions for turtle conservation (Appendix 1). The accelerated pace of human-caused environmental changes (i.e., global warming, habitat destruction, and modification), as well as the direct exploitation of different turtle species, is threatening populations and producing changes in their geographical distribution. It is therefore essential to obtain information that will allow a rigorous assessment of the threat category of each species, to identify priority areas for protection, and to design and implement conservation and management programs. Accordingly, it will be necessary to focus efforts on the implementation of studies of population ecology, reproductive ecology, movement patterns, and habitat use, as well as further studies on systematics and ecology, using molecular tools.

Habitat Use and Population Ecology

It is important to obtain information on basic biological characteristics of continental turtles, such as habitat use and spatiotemporal patterns of movement. This information will not only be biologically interesting but also will help define the resource needs and spatial habitat requirements of each species; information critical for determining which areas should be prioritized for protection to ensure the survival of their populations. Only protecting a portion of the habitat required for portions of the life cycle (e.g., nesting), without protecting all critical habitat, may be fruitless. Gallego-García (2012) provided a detailed review of studies on movement patterns and home ranges of Colombian turtles, highlighting the limited amount of knowledge available on this subject.

One of the largest knowledge gaps identified in our analysis concerned aspects of population ecology. Demographic parameters such as longevity and generation time, specific survival rates for different age or size classes and gender, growth rates in natural

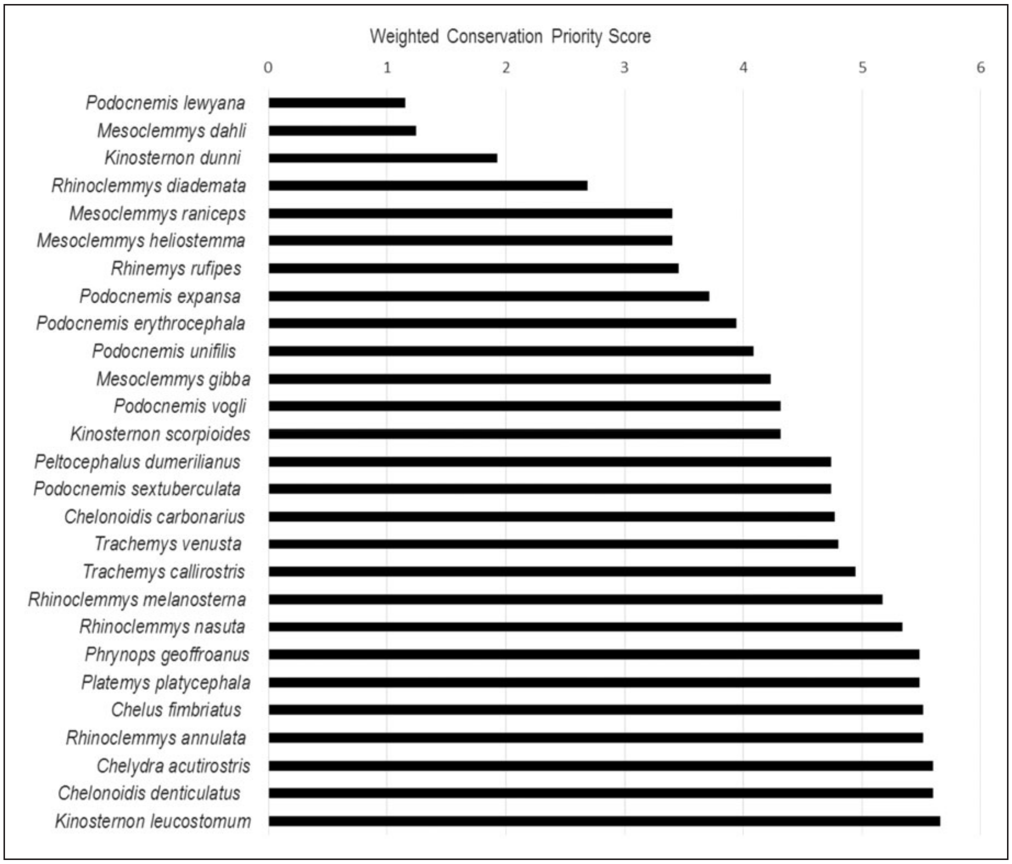

Figure 2. Classification of the species of continental turtles of Colombia by priority for conservation (lower values imply a greater priority; the maximum value is 6).

conditions, and fertility rates (nesting frequency, number of clutches per season, success rate for natural hatching) are known for very few species. There are abundance estimates available for a few species (*M. dahli*, *K. scorpioides albogulare*, White-lipped Mud Turtle: Kinosternon *leucostomum*; Ceballos, Zapata, Alvarado, & Rincón, 2016; Forero-Medina, Cárdenas-Arévalo, & Castaño-Mora, 2011; Forero-Medina, Castaño-Mora, & Montenegro, 2006) expressed as either density estimates or population size estimates. These parameters are not sufficient for assessing the long-term viability of populations (probability of extinction under various scenarios) or for evaluating the success of management and conservation measures (Crouse, Crowder, & Caswell, 1987; Crowder, Crouse, Heppell, & Martin, 1994; Heppell, Crowder, & Crouse, 1996). Thus, long-term monitoring studies are needed for more species, given that generation time is known for only one species, the longevity of no species is known, and only for *R. nasuta* and *P. lewyana* are there published data on survival rates. For *P. lewyana*, there are also data on fertility rates (Garcés-Restrepo, Giraldo, & Carr, 2014; Giraldo, Garcés-Restrepo, Carr, & Loaiza, 2012b; Páez et al., 2015).

Molecular Systematics and Conservation Genetics

Phylogenetic studies are important tools for biodiversity conservation, even though they are still little-used for this purpose (Mace & Purvis, 2008; Winter, Devictor, & Schweiger, 2013). Specifically, they seek to integrate information on phylogenetic relationships as a legacy of evolutionary processes (i.e., speciation and radiation) into conservation evaluations and actions (Erwin, 1991; Winter, Devictor, & Schweiger, 2013). Phylogenetic diversity studies may provide answers to significant questions concerning the extinction risks of a species or the definition of conservation priorities (Purvis, Agapow, Gittleman, & Mace, 2000; Winter, Devictor, & Schweiger, 2013), among others. For example, the concept of ''phylogenetic rarity'' (which refers to phylogenetic *uniqueness*; Brooks et al., 2006; Schweiger, Klotz, Durka, & Kühn, 2008) may help identify priority species for conservation. Additionally, at the level of phylogeography and population genetics, genetic studies permit the identification of ESUs that may correspond to unrecognized, cryptic species, or the identification of independent management units (ESUs and MUs, respectively; sensu; Moritz, 1994). These designations are based on

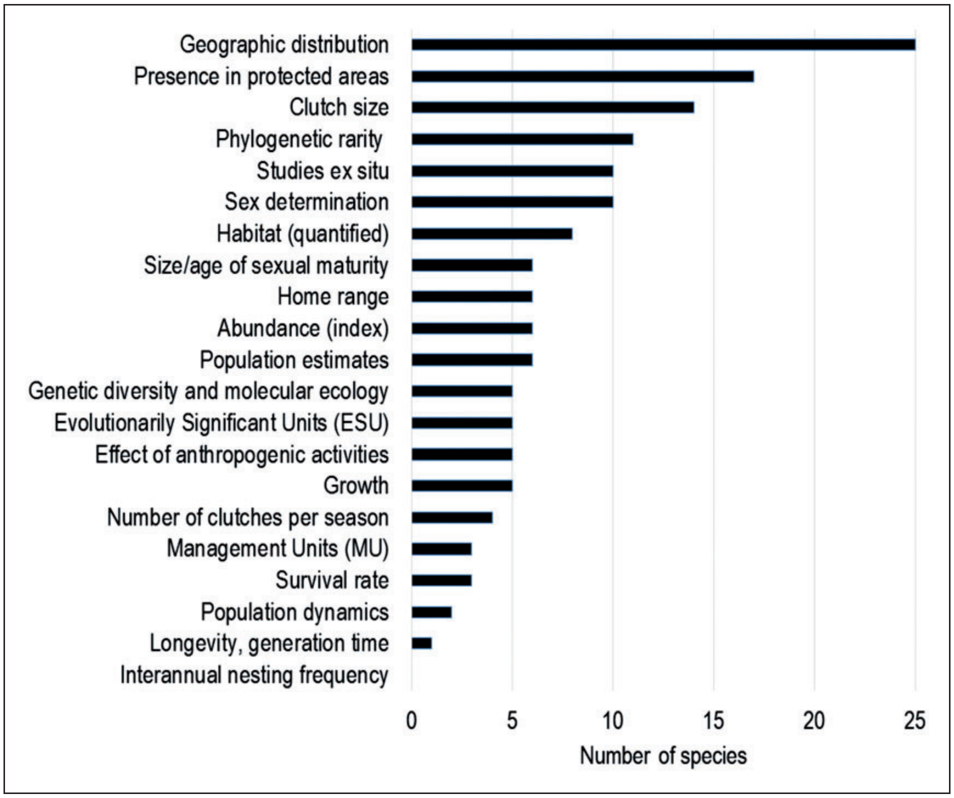

Figure 3. Level of knowledge for each criterion.

evidence of deep divergences and monophyly revealed by mitochondrial molecular markers, as well as differences in allele frequencies revealed by variable nuclear molecular markers (usually microsatellites) for ESUs, while MUs are distinguished based on differences in allele frequencies between populations (which reveal their demographic independence). Additionally, this type of research has allowed the measurement of genetic variation within populations, clarifying historical events and processes that may have influenced genetic diversity and genetic structure and allowing evaluation of the conservation value of populations or geographic areas from an evolutionary perspective.

Conservation priorities usually are identified at the species level, with undescribed species or differentiated genetic units being ignored (Vieites et al., 2009). However, there is an increasing trend to assign priorities at different levels of molecular differentiation, thereby taking taxonomic uncertainties into account when designing conservation actions (e.g., ESUs; MUs; putative species, Smith, Fisher, & Hebert, 2005; unconfirmed candidate species [UCS], confirmed candidate species [CCS], deep conspecific lineages [DCL]; Vieites et al., 2009).

For over a decade, researchers have been carrying out studies within these disciplines on the continental turtles of Colombia. Even though few in number, these studies have provided valuable insights and concrete recommendations for planning of conservation and management strategies. For example, research on the molecular phylogeny of the family Podocnemididae (Vargas-Ramírez, Castaño-Mora, & Fritz, 2008) and the Neotropical genus *Rhinoclemmys* (Le & Mccord, 2008; Vargas-Ramírez, Carr, & Fritz, 2013) revealed ancestral species that live in Colombia, species that deserve special attention as conservation objectives. Additionally, phylogeographic and population genetics studies have defined ESUs and MUs for the species *C. carbonarius* (Vargas-Ramírez, Maran, & Fritz, 2010), *R. melanosterna* (Vargas-Ramírez et al., 2013), *P. expansa* (Valenzuela, 2001; Pearse, Dastrup, Hernandez, & Sites, 2006), *P. lewyana* (Vargas-Ramírez, Castaño-Mora, Stuckas, & Fritz, 2012), and *P. unifilis* (Bock, Páez, & White, 2001; Escalona et al., 2009). Several of these studies also reported information related to genetic diversity within these species, as well as identifying ecological factors associated with population size, population bottlenecks, gene flow, natal philopatry, and population expansion in different spatiotemporal settings. However, the number of studies in these disciplines has been limited; therefore, it would be a priority to conduct further research on Colombian species of continental turtles, especially those with some degree of threat. Additionally, it will be desirable to conduct research within the realm of conservation genomics (Vargas-Ramírez, in press).

Effects of Human Activities, Geographic Distribution, and Other Gaps

Although for nearly every species, there is evidence that human exploitation and habitat degradation pose threats (Morales-Betancourt et al., 2015a; Morales-Betancourt, Lasso, Trujillo, & De La Ossa, 2012c), for very few species has the effect of different human activities been quantified in terms of its influence on population dynamics or individual fitness. While progress has been made in improving our knowledge of the geographic distributions of continental turtle species in Colombia (Montes-Correa, Saboyá-Acosta, Páez, Vega, & Renjifo, 2014; Ortíz-Yusty, Restrepo, & Páez, 2014; Páez et al., 2012a; Forero-Medina, Yusti-Muñoz, & Castaño-Mora, 2014), we are still not sure, for example, if other species reported in neighboring countries also occur in Colombia, as is the case with Zulia Toad-headed turtle: *Mesoclemmys zuliae* and Spot-legged Turtle: *Rhinoclemmys punctularia* (Rueda-Almonacid et al., 2007). Therefore, it is also a priority to continue exploring border areas to confirm that other species really are present in Colombia.

There is reasonably solid information about the presence of turtle species in protected areas (Forero-Medina et al., 2014) and on general reproductive biology such as clutch size, egg size, or the mechanism of sex determination (Ceballos, Romero, Saldarriaga, & Miranda, 2014; Leguízamo-Pardo & Bonilla-Gómez, 2014; Páez, 2012; Valenzuela & Ceballos, 2012). Nevertheless, this knowledge is not complete for all species or has only been documented in one population of the species. Consequently, these topics should not be excluded from future studies, especially with other species or different populations of species that have already been studied (Appendix 1).

The species of highest conservation priority corresponded with the three endemic species in Colombia, plus the two least-known species. In our priority ranking system, we considered ignorance as a variable to be included in determining conservation priorities. Endemic species are conservation priorities because the responsibility for their persistence rests solely on Colombian authorities and people. Ironically, none of these three endemic species has ranges that include national-level protected areas, such as a national park. This makes it essential to develop management strategies that promote the establishment of protected areas within their ranges to help ensure that these species persist (Forero-Medina, Cárdenas-Arévalo, & Castaño-Mora, 2012a; Morales-Betancourt et al., 2015b; Rentería-Moreno, Forero-Medina, Garcés-Restrepo, Carr, & Rueda-Almonacid, 2012; Vargas-Ramírez et al., 2012).

The research priorities that we identified did not coincide with the conservation priorities we identified. It is clear that in many cases, it is not necessary to have extensive knowledge of all aspects of the biology or ecology of a species in order to define strategies and implement conservation actions. This is especially true for conservation actions such as establishing protected areas, environmental education, and reduction of direct threats (human consumption, illegal traffic, etc.). Other management actions require a better understanding of the ecology of a species in order to be cost effective. In the case of most Colombian continental turtles, it is urgent to implement some form of conservation action. Thus, we recommend the adoption of a strategy of adaptive management capable of implementing pro-active steps while increasing knowledge of the biology of the target species; in that way, newly acquired information (and that derived from monitoring) may provide continuous feedback for the conservation efforts (Nichols & Williams, 2006).

We recognize that there are multiple approaches for selection of priority species to direct conservation efforts. Our approach is one of many that seek to identify species and topics that require more attention urgently. Nevertheless, we hope that our priority classification results may help stimulate research and conservation efforts for the continental turtle species of Colombia where they are most needed (Morales-Betancourt et al., 2015b).

Implications for Conservation

Given the limited funds for turtle conservation in many South American countries, including Colombia, it is sometimes necessary to have an objective way of prioritizing species. We believe that our work provides managers a useful set of recommendations for allocating limited funds and addressing the threats for the most critical species in Colombia. Our work can help define which species require management plans and investment from governmental agencies, for example. On the other hand, the research priorities identified can help researchers and students identify particular topics that are least studied and are more necessary for producing conservation recommendations. It is necessary to direct human and economic efforts toward those issues that are high priorities. In this regard, we consider it essential to promote short- to medium-term studies in ecology and molecular systematics, as well as medium- to long-term demographic studies that will be biologically representative and upon which conservation and management efforts may be based. The research challenges for Colombian continental turtle species are great because they involve leaving our geographic and thematic comfort zones to take on the difficulty of gaining access to the lesser known species, developing studies that require great effort in the field for long periods, and that combine the expertise of ecologists, taxonomists, and molecular biologists, among others.

Appendix 1. Knowledge Level by Species for Each of the 21 Criteria.

	Vernacular name	Species	Geographic range	Pop. estimates	Abundance (index)	Home range	Habitat	Population dynamics	Growth	Size or age of sexual maturity	Longevity, generation time	Sex determination	Number of clutches per season	Clutch size	Interannual nesting frequency	Survival rate	Presence in protected areas	Effect of human activities	Studies ex situ	Phylogenetic rarity	Evolutionarily Significant Units	Management Units	Genetic diversity or molecular ecology	Total
1	Big-Headed Amazon River Turtle	*Peltocephalus dumerilianus*	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0	5
2	Magdalena River Turtle	*Podocnemis lewyana*	1	1	1	0	1	1	1	1	1	1	0	1	0	1	0	1	1	1	0	1	1	16
3	Savanna Side-Necked Turtle	*Podocnemis vogli*	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	4
4	Red-Headed Amazon River Turtle	*Podocnemis erythrocephala*	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0	5
5	Giant South American River Turtle	*Podocnemis expansa*	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	1	1	1	1	11
6	Six-Tubercled Amazon River Turtle	*Podocnemis sextuberculata*	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0	5
7	Yellow-Spotted Amazon River Turtle	*Podocnemis unifilis*	1	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	1	10
8	Colombian Slider	*Trachemys callirostris*	1	1	1	0	1	0	1	1	0	1	0	1	0	1	1	1	0	0	0	0	1	12
9	Meso-American Slider	*Trachemys venusta*	1	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	0	0	0	0	7
10	Dahĺs Toad-Headed Turtle	*Mesoclemmys dahli*	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
11	Black-Lined Toad-Headed Turtle	*Mesoclemmys raniceps*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	Gibba Toad-Headed Turtle	*Mesoclemmys gibba*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
13	Amazon Toad-Headed Turtle	*Mesoclemmys heliostemma*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(continued)

Continued

	Vernacular name	Species	Geographic range	Pop. estimates	Abundance (index)	Home range	Habitat	Population dynamics	Growth	Size or age of sexual maturity	Longevity, generation time	Sex determination	Number of clutches per season	Clutch size	Interannual nesting frequency	Survival rate	Presence in protected areas	Effect of human activities	Studies ex situ	Phylogenetic rarity	Evolutionarily Significant Units	Management Units	Genetic diversity or molecular ecology	Total
14	Geoffroy's Side-Necked Turtle	*Phrynops geoffroanus*	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	3
15	Red Side-Necked Turtle	*Rhinemys rufipes*	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
16	Twist-Neck Turtle	*Platemys platycephala*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	3
17	Mata Mata	*Chelus fimbriatus*	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	4
18	White-Lipped Mud Turtle	*Kinosternon leucostomum*	1	0	1	0	1	0	0	1	0	0	1	1	0	0	1	1	1	0	0	0	0	9
19	Dunn's Mud Turtle	*Kinosternon dunni*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
20	White-Throated Mud Turtle	*Kinosternon scorpioides*	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	4
21	South American Snapping Turtle	*Chelydra acutirostris*	1	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	7
22	Brown Wood Turtle	*Rhinoclemmys annulata*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	4
23	Maracaibo Wood Turtle	*Rhinoclemmys diademata*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	3
24	Colombian Wood Turtle	*Rhinoclemmys melanosterna*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	6
25	Chocoan River Turtle	*Rhinoclemmys nasuta*	1	1	1	0	1	1	1	1	0	0	0	1	0	1	1	1	0	1	0	0	0	12
26	Red-Footed Tortoise	*Chelonoidis carbonarius*	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	0	0	6
27	Yellow-Footed Tortoise	*Chelonoidis denticulatus*	1	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	7
	Total		25	6	6	6	8	1	4	6	0	10	4	14	0	2	17	5	10	11	5	3	5	

Note. 0 = *no studies exist*; 1 = *there is at least one study.*

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