REVIEW

Distribution, habitat and adaptability of the genus Tapirus

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Abstract

In this manuscript, as a starting point, the ancient and current distribution of the genus *Tapirus* are summarized, from its origins, apparently in Europe, to current ranges. Subsequently, original and current tapir habitats are described, as well as changes in ancient habitats. As the manuscript goes on, we examine the ways in which tapir species interact with their habitats and the main aspects of habitat use, spatial ecology and adaptability. Having reviewed the historic and current distribution of tapirs, as well as their use and selection of habitats, we introduce the concept of adaptability, considering that some of the tapir physiological characteristics and behavioral strategies can reduce the negative impact of habitat alteration and climate change. Finally, we provide recommendations for future research priorities. The conservation community is still missing important pieces of information for the effective conservation of tapirs and their remaining habitats in Central and South America and Southeast Asia. Reconstructing how tapir species reached their current distribution ranges, interpreting how they interact with their habitats and gathering information regarding the strategies they use to cope with habitat changes will increase our understanding about these animals and contribute to the development of conservation strategies.

Key words: adaptability, climate change, distribution, habitat, Tapirus

INTRODUCTION

Tapirs are descended from an ancient group of animals related to primitive horses and rhinoceroses, and were very abundant and diverse in the later Eocene, especially in North America and Asia. Ancestors of mod-

Correspondence: Manolo J. García, Centro de Estudios Conservacionistas, Universidad de San Carlos de Guatemala, Avenida Reforma 0-63 zona 10, Guatemala City, Guatemala. Email: garcia.manolo@usac.edu.gt ern tapirs radiated during the Late Oligocene and Early Miocene, but became extinct in most of their range during the Late Pleistocene. Current tapir species belong to the genus *Tapirus*, apparently originated in Europe during the Oligocene and later dispersed to Asia, North America and South America. At present, the genus has 4 living species, 1 in Asia and 3 in Central and South America; all of them are greatly endangered, primarily due to habitat loss and hunting over their whole distribution ranges. Present habitats include mostly tropical forests associated with water and riparian environments. To delineate effective conservation strategies for living tapir species, it is necessary to understand the intimate relationship between tapirs and their habitat in order to provide valuable knowledge to predict future tapir habitat requirements, which, in turn, can substantiate predictions in terms of adaptability. There is still much information lacking; however, the data currently available can provide the baseline to guide the development of conservation strategies and policies aimed at improving our ability to face current and future challenges for tapir conservation. This manuscript contributes to the construction of this baseline, providing an outline of the distribution, habitat use and adaptability of tapirs.

DISTRIBUTION OF TAPIRS

Present tapir species have a discontinuous distribution as a result of environmental changes, and consequent migration events of their ancestors, over time. The past and present distribution of the genus Tapirus is reviewed to highlight its dynamic nature, an important issue to consider for management and conservation planning. Primitive tapirs were distributed through North America, Europe and Asia. The oldest record of the genus Tapirus was found in Europe from the Oligocene. During the Miocene, the genus was affected by a global reduction of forest cover, as a consequence of climate change, and dispersed throughout Europe, Asia and North America (Radinsky 1965). The distribution of tapirs in Europe persisted until the Pliocene (Hulbert 2005). The 3 distinct tapir mitochondrial lineages that led to the present 4 species, 2 Neotropical and 1 Asian, diverged approximately 20-30 Ma (Ashley et al. 1996). The oldest record found in North America is from the Middle Miocene, and in South America from the Early Pleistocene (Hulbert 2005; Ferrero & Noriega 2007). In North America, tapirs were still present from California to Florida until approximately 11 000 years ago, only becoming extinct during the Pleistocene (Hulbert 2005).

Tapir species dispersed southward from North America when Central America emerged and formed a bridge that enabled the Great American Interchange between the North and South. Studies using mitochondrial cytochrome c oxidase subunit II and gene 12S rRNA sequences indicate a close relationship between the lowland tapir [*Tapirus terrestris* (Linnaeus, 1758)] and the mountain tapir [*Tapirus pinchaque* (Roulin, 1829)], both species corresponding to 1 of the Neotropical lineages, suggesting a single colonization to South America (approximately 2–3 Ma) (Ashley *et al.* 1996; Norman & Ashley 2000). The mountain tapir is distributed throughout the Andean regions of Colombia, Ecuador and Peru in South America, restricted to mountain ecosystems, at altitudes from 2000 to 4500 m (Lizcano et al. 2002). The lowland tapir has the broadest geographic distribution of all tapirs (11 range countries and 21 different biomes throughout South America), occupying tropical lowlands (0-1200 m), including the Amazon and Orinoco basins, Chaco forests of Bolivia and Paraguay, Atlantic Forests of Brazil and areas of northern Argentina (Padilla & Dowler 1994; Taber et al. 2008; Medici 2010). The second Neotropical lineage is represented by Baird's tapir [Tapirus bairdii (Gill, 1865)], which might be a late migrant from North America, distributing along Central America from southern Mexico to Colombia (0-3620 m; Naranjo & Vaughan 2000). Tapirs belonging to the Asian lineage reached Southeast Asia during the Pliocene (Tong et al. 2002) and were ancestors of the Malayan tapir (Tapirus indicus Desmarest, 1819), which had its origin in the continental landmass but is currently present on some islands. It is found in southern Thailand and Myanmar (Burma) through the Malayan Peninsula and the southern part of the island of Sumatra, Indonesia. Some fossil records also indicate that the species previously occupied Java and Borneo (Cranbrook & Piper 2009).

CHANGING HABITATS

The true tapiroids, ancestors of modern tapirs, radiated during the Late Oligocene and Early Miocene. Since then, distribution of tapirs has changed through time. These changes were caused by migrations, topography, climate change and the resulting distribution of forests. According to Janis (1993), patches of tropical forest must have acted as refugees during the Miocene, as evidenced by the persistence of specialized browsers, such as tapirs and peccaries, surviving today in Central and South America. During the Pleistocene, the phenomenon of extinction of all the megaherbivores (mammoths, mastodons, horses, sloths, glyptodonts and giant armadillos) and other large mammals (>44 kg) was probably associated with climate and environmental changes (MacFadden 2000). Today, taxa including llama, tapir and bison have greatly reduced ranges in comparison to their ranges 15 000 years ago (MacFadden 2000; Hoppe & Koch 2007). As temperatures lowered during the Pleistocene, there was a range retraction for mammal species adapted to warm and humid conditions (Tapiridae, Tayassuidae, Procyonidae and Echimyidae) and

species adapted to colder and more arid environments appeared (Cione *et al.* 2007). In addition to climatic change, the emergence of *Homo sapiens* Linnaeus, 1758 resulted in a 'Pleistocene overkill' of large prey, accelerating the extinction of endemic families and many taxa (MacFadden 2000; Cione *et al.* 2007).

Environments where ancient tapirs lived seem to be analogous to the ones where modern species are found today: tropical forests in warm and wet climates, generally associated with water bodies and wetlands (Eisenmann & Guérin 1992), such as evergreen, sub-deciduous and deciduous tropical forests, cloud forests, marshes, swamps and mangroves (Holden *et al.* 2003). Today's habitats represent places of refuge for tapirs as well as for other fauna and flora species. These habitats show significant biological diversity, which is related to a history of migrations, continental shifts and climate change.

HABITAT AND FEEDING ECOLOGY

Habitat use and selection

Several studies have identified patterns of habitat preference and selection in tapirs. There is growing evidence that tapirs have large spatial requirements and also require certain habitat types, and habitat quality, that contain the resources they need (or prefer) to survive and persist in the long term (Medici 2011). Data on habitat use and habitat selection provides valuable information on the requirements and strategies tapir individuals use to survive, allowing us to learn more about past and present tapir species and generates critical data to model conservation and management strategies based on possible future scenarios.

It is known that ancient tapirs were browsers, just as the current species are. Therefore, we expect a similar pattern in terms of habitat use. Studies have shown that all 4 tapir species select their habitats according to 2 main factors: availability of food and water resources (Salas & Fuller 1996; Foerster & Vaughan 2002; Naranjo 2009). Tapirs are, in general, closely associated with riparian forests, marshes, lakes and streams, where they spend most of their active time and perform most of their activities, particularly foraging (Medici 2010). All 4 tapir species depend on water for protection against predators (jaguars and pumas in South and Central America and tigers in Southeast Asia) and regulation of body temperature during the hottest hours of the day. Tapirs also use water for resting, sleeping and defecating (Terwilliger 1978; Naranjo 1995a; Algers *et al.* 1998).

In general, secondary forests are preferred, especially for foraging, due to the high rate of production of young steams stimulated by increased luminosity (Naranjo 1995a; Salas 1996; Tobler 2002). Medici (2010) reports riparian and tall mature forests to be the most represented habitat type within the lowland tapir's home ranges in the Brazilian Atlantic Forest. In the Central Andes of Colombia, Lizcano and Cavelier (2000) found that mountain tapirs use more primary forest when compared to other habitats, which was also observed for Baird's tapirs in Corcovado National Park, Costa Rica (Foerster 1998). Altered habitats, for example for agriculture, palm oil plantations and pasture, are usually avoided by tapirs, and the expansion of these types of land-use are considered to be a major threat to wild tapir populations (Gemita et al. 2007; Medici 2010). Trails for tourism and highly disturbed areas were found to be avoided by Baird's tapirs in the Sierra Madre of Chiapas and the Lacandon Forest, Mexico (Lira Torres et al. 2004; Tejeda-Cruz et al. 2009).

Palm forests are important tapir habitat given that their fruits are crucial food resources for tapirs. Several studies have demonstrated the intensive use of palm forests and high percentages of consumption of palm fruits by lowland tapirs. In the Atlantic Forests of Brazil, lowland tapirs are known to use patches of Jerivá palm (Syagrus romanzoffiana) very intensively (Olmos 1997; Olmos et al. 1999; Galetti et al. 2001; Tófoli 2006). In the northeastern region of the Brazilian Pantanal, tapirs show a high preference for Acuri palm forests (Scheelea phalerata) when compared to other vegetation types (Cordeiro 2004). In the Amazon, patches of Mauritia flexuosa are frequently visited by lowland tapirs (Bodmer 1990; Tobler 2008). Accordingly, potential tapir distribution models demonstrate high occurrence probabilities in such habitat areas.

Resting sites

Tapirs seek sheltered sites for resting during the day, the most common being in tree roots or shaded forests and thickets (Padilla & Dowler 1994; Acosta *et al.* 1996; Algers *et al.* 1998). Lowland tapirs in the Atlantic Forests of Morro do Diabo State Park (MDSP), Brazil appeared to use the same resting sites repeatedly over long periods of time, with short movements of just a few meters, apparently looking for shade (Medici 2010). In Barro Colorado Island, Panama, as well as in Corcovado National Park, Costa Rica, Baird's tapirs were observed resting in mud-holes to which they returned several times (Terwilliger 1978; Naranjo 1995a; Foerster 1998). In contrast, in the Cordillera de Talamanca, Costa Rica, Tobler (2002) found that tapir sleeping places were only used a few times.

Defecating sites

Tapirs usually defecate in water, typically shallow ponds or river streams (Naranjo 1995b, 2009). Of 136 Baird's tapir fecal samples collected in Corcovado National Park, Costa Rica, 94% were found in or near permanent or seasonal water bodies, whereas only 6% of the samples were found on dry land. Some studies have found that tapirs use 'latrines', consisting of large concentrations of dung piles in the same location (Naranjo & Cruz-Aldán 1998; Fragoso *et al.* 2003; Tófoli 2006). Latrines are believed to be seasonal and some might be used for many years (Acosta *et al.* 1996). Latrines might be used by one or several individuals. Depending on climate conditions, decomposition of feces can take 3 to 4 months (Tobler 2002).

Salt licks

Several studies have reported the use of salt licks by tapirs. Salt licks are natural areas with high concentrations of salts, where tapirs and other animals consume minerals by licking them directly from the ground, eating clay or drinking water in ponds or pools (Montenegro 1998; Lizcano & Cavelier 2004; Novarino et al. 2004; Tobler 2008). This behavior might be a response to low availability of minerals in the ecosystem, especially nitrogen and sodium, and should help tapirs fulfill their mineral requirements, as well as neutralize toxins from some of the plant species consumed as part of their diet (Acosta et al. 1998; Lizcano & Cavelier 2000, 2004). Tapir visits to salt licks can last between a few minutes to more than an hour (maximum of 190 min observed for T. pinchaque in Colombia). The same salt lick can be visited by many individuals in 1 night (Lizcano & Cavelier 2004). In some cases, tapirs walk several kilometers to visit salt licks (Tobler 2008).

Paths

One of the most characteristic behaviors of tapirs is the use of well-worn trails or paths to move from resting to foraging and defecating areas (Terwilliger 1978; Naranjo 1995a; Acosta *et al.* 1996; Tobler 2008; Medici 2010). This results in a path system, including main trails, each with ramifications connecting to smaller trails.

Feeding ecology

Tapirs are exclusively herbivorous. They have a broad diet, feeding on a bewildering array of plant species and many different plant parts, including saplings, ferns, vines, palms and trees and their roots, young stems, twigs, leafs, bark, flowers, fruits and seeds (Williams 1980; Naranjo 1995b; Salas & Fuller 1996; Naranjo & Cruz-Aldán 1998; Henry *et al.* 2000; Downer 2001; Naranjo & Bodmer 2002; Tobler 2002, 2008; Tófoli 2006; Bachand *et al.* 2009; Talamoni & Assis 2009; Zorzi 2009).

Although tapirs are essentially browsers, they consume fruit extensively when available (Bodmer 1990). Tófoli (2006) show that the diet of lowland tapirs in the Atlantic Forest of MDSP in Brazil consists of 37% fruit/seed and 63% leaf/fiber. Bodmer (1990) analyzed stomach, cecal and fecal samples of lowland tapirs in the Peruvian Amazon and reported that the species consumed 33% fruit and 66% leaf/fiber. It has been suggested that tapirs consume fibrous vegetation for protein and depend on more digestible foliage and fruit for energy (Foose 1982). Tapirs may consume many different plants but generally there is a small group of species that represent most of the biomass consumed. Although the diet of tapirs has been studied in several locations, very little is known about the nutritional contents of food items consumed by tapirs in the wild. Depending on the availability of different food items, tapirs can shift their foraging strategy among habitat types and seasons.

The extensible proboscis is used to strip leaves and pluck fruits. Fruit may be taken from low shrubs or as fallen fruit on the ground. Tapirs will occasionally stand on their hind feet and reach with their prehensile proboscis over 2 m from the ground to obtain food. Plants are consumed regardless of thorns or insects (Terwilliger 1978). Tapirs have many different foraging strategies. Most of the species have been reported to have foraging areas, and to forage while walking, taking specific plant species from both sides of their path (Medway 1974). Zigzag browsing patterns are reported for Baird's tapir by Terwilliger (1978) in Panama. Foraging areas of Baird's tapir have been observed in natural open areas close to rivers where the high penetration of light and availability of water ensures constant availability of food sources (García 2006; Naranjo 2009).

ACTIVITY PATTERNS

Tapirs are mostly crepuscular/nocturnal, generally presenting 2 peaks of activity, 1 before the sunrise and a second after sunset, and differences among sites might be related to human pressure (Lizcano & Cavelier 2000; Foerster & Vaughan 2002; Holden *et al.* 2003; Novarino *et al.* 2004; Medici 2010). Tapirs are largely inactive in the middle of the day, which corresponds to the hottest hours of the day (Medici 2010). In MDSP, peaks of activity seemed to correspond to movements between resting and foraging sites using well-worn paths, as mentioned above (Medici 2010). In some cases, activity patterns might vary among sexes (females being more active than males) and age classes (adults being more active than sub-adults) (Medici 2010).

SPATIAL ECOLOGY AND INTRA-SPECIFIC INTERACTIONS

Tapirs are wide-ranging species. Although the spatial requirements of tapirs vary with the carrying capacity of different habitats found within their distribution range, they usually require considerably large home ranges.

Home range sizes have been estimated for the 4 tapir species using different methods, including mainly radio telemetry, line transect sampling, camera traps and footprint identification techniques (Foerster & Vaughan 2002; Downer 2003; Noss et al. 2003; Lizcano & Cavelier 2004; Naranjo 2009; Medici 2010). Tapir home range estimates vary widely due to the different methods applied and the different environments studied. Home ranges also vary within individuals in the same area. Medici (2010) recorded home ranges from 1.1 to 14.2 km² for lowland tapirs during a 12-year study in MDSP. Mountain tapir individuals might have extensive home ranges because of daily movements coming down the mountains to access water and then climbing back to higher elevations. The mean home range size of mountain tapirs has been estimated to be approximately 2.50 km² (Lizcano 2006). Baird's tapirs appear to use smaller areas when compared to the other 2 Neotropical species. A previous estimate of the home range size for Baird's tapirs is 1.25 km² (Foerster 1998; Foerster & Vaughan 2002). Malayan tapirs have the largest home ranges of all tapir species, usually over 10 km² (Abdul-Ghani 2009). Day and night home ranges might differ, with less activity during the day.

Sub-adult tapirs might have larger home ranges than adults due to dispersal movements. The tapir calf stays with its mother for approximately 12–18 months (Foerster & Vaughan 2002; Medici 2011). Once they separate, young Baird's tapirs in Corcovado National Park, Costa Rica stay in the vicinity of the mother's home range for 3–4 years prior to dispersal from the area and establishment of their own home ranges (Foerster & Vaughan 2002). This provides some evidence that the spatial and social organization of tapirs might be associated with the relatedness among different individuals, which most probably leads to an increased level of tolerance among neighbors (Medici 2010).

The structure of the tapir home range is very complex, including multiple core areas of use that are established according to the distribution of patches of preferred habitats (Tobler 2008; Medici 2010). Large, highly mobile animals such as tapirs likely have a greater perceptual range (Zollner 2000), thereby being able to detect suitable habitat and perceive landscape structure and interrelatedness (Wiens 1989). In MDSP, the number of core areas of use within the lowland tapir home range was as high as 17 units at the 50% core level, with as many as 9 units at the 25% level. When summed up, the total size of the core areas of use comprised very small portions of the tapir home ranges (50% core areas comprised approximately 17% of the home range and 25% core areas comprised no more than 6%) (Medici 2010).

There is no concrete evidence of territoriality by tapirs. Lowland tapirs in MDSP show strong home range overlap (average of 37%) between neighboring individuals (Medici 2010). The same has been observed for Baird's tapirs in Corcovado National Park, Costa Rica (Foerster 1998). Nevertheless, both male and female tapirs can spray urine, which is believed to be used for territory marking (Terwilliger 1978). Tobler (2008) observed that lowland tapirs monitored through GPS telemetry in the Peruvian Amazon regularly walked along the boundaries of their home ranges, most probably defining their territory against other individuals by maintaining clear home range boundaries.

ADAPTABILITY

Tapirs come from a linage that has been facing environmental changes over the past million years, and, consequently, today have greatly reduced ranges when compared to their ranges 15 000 years ago (MacFadden 2000). The survival of living tapir species relies on their ability to adapt to current and future environmental conditions, including human alterations to habitats. This adaptation is related to their physiological characteristics and the strategies used by the species. As mentioned above, availability of food and water are important factors for tapir habitat selection and adaptability might be related to the availability of these resources, as well as to the neutralization of major habitat threats.

Baird's tapir forages heavily on Chusquea at a cloud forest in Costa Rica (Naranjo & Vaughan 2000; Tobler 2002), but prefers Melanthera (Asteraceae) and Psychotria (Moraceae) in Guatemala (García 2006). In addition, Baird's tapirs show seasonal variations in diet content, as well as in the distances traveled searching for food, optimizing the effort according to the energy obtained from available food sources (Naranjo 1995b). The tapir ability to adapt to different diets might be related to physiological characteristics. Seasonal variations in diet are strategies used to increase chances of survival. Species with a more selective diet, such as the Malayan tapir (Medway 1974), might be more vulnerable than the more generalist species, such as Baird's tapir (Terwilliger 1978). Seasonal variations in diet probably have to follow variations in flowering and fruiting seasons resulting from climate change. Therefore, modifications in forest plant composition caused by anthropogenic disturbances and climate change will be a crucial issue for the survival of tapir species in the near future.

Water is also a major issue for tapirs. Tapirs depend heavily on water and might even reduce their home ranges during the dry season, staying closer to permanent water bodies. If global temperatures increase according to the levels that have been predicted, we can expect tapirs to be even more dependent on water to regulate their body temperature. Drier habitats, such as the Maya Forest shared by Mexico, Guatemala and Belize, where tapirs and other species show a great dependence on the remaining bodies of water during the dry season, will be more vulnerable. In addition, it has been projected that the quality of inland water bodies will be reduced and drought seasons will increase (Bates et al. 2008), which could have an amplifying effect, making some populations more vulnerable than others. In addition, more shaded areas will be needed for sheltering and resting purposes.

Altitudinal distribution may be affected as well, especially for mountain tapirs, which occur in narrow al-

titudinal ranges. If global temperatures increase, distribution areas of habitats will likely shift to different altitudes, forcing tapirs to migrate; other tapir species have wider altitudinal ranges (0–3620 m for Baird's tapir, 0–1200 m for lowland tapir and 0–2400 m for Malayan tapir) (Naranjo & Vaughan 2000; Holden *et al.* 2003). Changes in altitudinal ranges of South American tapir species may induce the overlap of distribution ranges and, consequently, hybridization between species might occur.

One might say that tapirs will find a way to cope with climate change, as they have been doing for the past million years; however, threats related to humans, such as habitat loss, habitat fragmentation and hunting, could potentially override the effects of climate change, making it impossible for tapirs to cope.

Habitat loss is largely the result of the transformation of natural areas into pasture, agricultural crops and urban centers. Over the years, these processes have altered continuous natural habitats, along with their natural boundaries and transitions, into human-delimited landscapes, affecting wildlife in many different ways and bringing a massive number of species to the brink of extinction. Large mammals, such as tapirs, are especially susceptible to this form of habitat loss (Kinnaird *et al.* 2003).

Habitat loss and fragmentation have reduced and isolated tapir populations worldwide and have also increased their vulnerability to other human disturbances. Fragmentation prevents natural ecosystems from responding to climate change, given that natural corridors for animal and plant flows are altered or interrupted. Species such as tapirs might not be able to migrate to areas with more favorable conditions if the distribution of forests is modified. In addition, while crossing humanaltered landscapes, tapirs are heavily impacted by other threats, such as increased predation, hunting, roadkill and infectious diseases from domestic livestock, all of which override the impact of fragmentation, strongly affecting the likelihood of extirpation of remaining tapir populations (Bodmer et al. 1997; Cullen et al. 2000; Medici 2011). Persistent unregulated hunting is a major threat to tapirs (Brooks et al. 1997). The 4 tapir species have very slow reproductive rates and small populations show rapid declines and slow recoveries when hunted. Tapirs become more evasive in areas with high hunting pressure, staying away from areas with human presence and changing patterns of activity to avoid contact with humans (Lira Torres et al. 2004).

FUTURE RESEARCH PRIORITIES

Although there is good quality data and information available on tapirs, some basic knowledge is still lacking in many range countries. Diet, habitat use, habitat selection, spatial ecology, intra-specific interactions, population demography, reproductive parameters and even up-to-date presence/absence data is lacking for many localities. These very basic pieces of information are crucial for modeling the current status, viability and risk of extinction for tapir populations, as well as predicting the effects of climate change and other future scenarios. Good quality spatial information related to tapirs and their habitats is essential for the development of these models. Methodologies involving radio telemetry techniques appear to be appropriate for collecting this kind of data. The relationship between tapirs and water bodies, including wetlands, must be better understood in order to include this feature into climate change effect models, especially in areas with low availability of superficial water or in areas susceptible to seasonal floods. It is important to implement monitoring programs focused on tapirs' habitat use and selection, and the physical and chemical characteristics of water bodies in these areas. Other important issues that must be investigated include the ability of tapirs to adapt to natural and induced changes in their environment and to survive, as well as the identification of the most critical and vulnerable habitat types. Existing potential distribution models can be combined with climate change projections to create scenarios of probable future distributions of the tapir species. The influence of habitat spatial patterns on tapirs' distribution and survival should be included in these scenarios. The effects of environmental variations on the phenology and distribution of important plant species included in the diet of tapirs could also be modeled; consequently, field data is also needed.

Researchers should be able to gather and provide this information to stakeholders, other researchers and conservation managers to substantiate the development of strategies, aiming at increasing the viability and persistence of tapir populations in the long term. Alliances and partnerships between different stakeholders, including researchers, national and international non-governmental organizations, universities, zoological institutions and governmental agencies in range countries, should be strengthened to develop regional and international strategies, and to implement coordinated actions. This would most certainly prove to be a significant contribution to the conservation of the 4 tapir species and their remaining habitats in Central and South America and Southeast Asia.

CONCLUSION

The distribution of tapirs has changed over time; therefore, for management and conservation purposes, it is essential to consider that distribution ranges are dynamic and current distribution areas should be expected to change in the future. The existing information on habitat use indicates a strong relation between tapirs and water bodies, including wetlands; consequently, changes involving modification of rainfall and superficial water availability are critical for the survival of tapirs. Habitat alteration caused by humans reduces the species capacity to respond to long-term and large-scale environmental changes. There is still much information lacking to predict the effects and responses of tapirs to future habitat and climate change, but existing information provides a general baseline guide.

REFERENCES

- Abdul-Ghani S (2009). Home range size, density estimation and behaviour of Malayan tapirs (*Tapirus indicus*) at Krau Wildlife Reserve (MSc thesis). University of Science Malaysia, Gelugor, Penang, Malaysia.
- Acosta H, Cavelier J, Londoño S (1996). Aportes al conocimiento de la biología de la danta de montaña, *Tapirus pinchaque*, en los Andes Centrales de Colombia. *Biotropica* 28, 258–66.
- Algers S, Vaughan C, Foerster CR (1998). Resting site microhabitat selection by *Tapirus bairdii* during the dry season in Corcovado National Park, Costa Rica. *Vida Silvestre Neotropical* 7, 136–8.
- Ashley M, Norman J, Strossl L (1996). Phylogenetic analysis of the perissodactylan family Tapiridae using mitochondrial cytochromec oxidase (COII) sequences. *Journal of Mammalian Evolution* **3**, 315–26.
- Bachand M, Trudel O, Ansseau C, Cortez J (2009). Dieta de *Tapirus terrestris* L. em um fragmento de Mata Atlântica do Nordeste do Brasil. *Revista Brasileira de Biociências* 7, 188–94.
- Bates BC, Kundzewicz ZW, Wu S, Palutikof JP, eds (2008). Climate change and water. Technical Paper of the Intergovernmental Panel on Climate Change, IPCC Secretariat, Geneva.

Bodmer RE, Eisenberg J, Redford K (1997). Hunting and the likelihood of extinction of Amazonian mammals. *Conservation Biology* **11**, 460–66.

Bodmer RE (1990). Responses of ungulates to seasonal inundations in the Amazon floodplain. *Journal of Tropical Ecology* **6**, 191–201.

Brooks D, Bodmer RE, Matola S (1997). *Tapirs: Status Survey and Conservation Action Plan.* IUCN/SSC Tapir Specialist Group. IUCN, Gland, Switzerland.

Cione A, Tonni E, Bargo S *et al.* (2007). Mamíferos continentales del Mioceno tardío a la actualidad en la Argentina: cincuenta años de estudio. In: Archangelsky S, Sanchez T, Tonni EP, eds. *Ameghiniana*, Edición Especial 50 Aniversario, Asociación Paleontológica Argentina, Buenos Aires, pp. 257–78.

Cordeiro J (2004). Estrutura e heterogeneidade da paisagem de uma unidade de conservação no Nordeste do Pantanal (RPPN SESC Pantanal), Mato Grosso, Brasil: efeitos sobre a distribuição e densidade de antas (*Tapirus terrestris*) e cervos-do-pantanal (*Blastocerus dichotomus*) (PhD dissertation). Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Brazil.

Cranbrook E, Piper P (2009). Borneo records of Malay tapir, *Tapirus indicus* Desmarest: a zooarchaeological and historical review. *International Journal of Osteo-archaeology* **19**, 491–507.

Cullen L, Bodmer RE, Valladares Padua C (2000). Effects of hunting in habitat fragments of the Atlantic Forest, Brazil. *Biological Conservation* **95**, 49–56.

Downer CC (2003). Ambito hogareño y utilización de hábitat del tapir andino e ingreso de ganado en el Parque Nacional Sangay, Ecuador. *Lyonia* **4**, 31–4.

Downer CC (2001). Observations on the diet and habitat of the mountain tapir (*Tapirus pinchaque*). *Journal of Zoology* **254**, 279–91.

Eisenmann V, Guérin C (1992). *Tapirus priscus* Kaup from the upper miocene of western Europe: palaentology, biostratigraphy and palaeoecology. *Paleontologia i Evolución* **24–5**, 113–22.

Ferrero B, Noriega J (2007). A new upper plestocene tapir from Argentina: remarks on the phylogenetics and diversification of Neotropical tapirridae. *Journal of Vertebrate Paleontology* **27**, 504–11.

Foerster CR (1998). Ecología de la danta Centroamericana (*Tapirus bairdii*) en un bosque lluvioso tropical de Costa Rica (MSc thesis). Universidad Nacional, Heredia, Costa Rica. Foerster CR, Vaughan C (2002). Home range, habitat use and activity of Baird's tapir in Costa Rica. *Biotropica* **34**, 423–37.

Foose T (1982). Trophic strategies of ruminant *versus* nonruminant ungulates (PhD dissertation). University of Chicago, Chicago, USA.

Fragoso JMV, Silvius KM, Correa JA (2003). Longdistance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology* 84, 1998–2006.

Galetti M, Keuroghlian A, Hanada L, Morato M (2001). Frugivory and seed dispersal by the lowland tapir (*Tapirus terrestris*) in southeast Brazil. *Biotropica* **33**, 723–6.

García M (2006). Caracterización de la dieta y el hábitat del tapir centroamericano (*Tapirus bairdii*) en el Parque Nacional Laguna Lachuá, Cobán, AltaVerapaz (BSc thesis). Universidad de San Carlos de Guatemala, Guatemala.

Gemita E, Hall A, Maddox T (2007). The Asian tapir in Jambi lowland forest and commercial landscape. *Tapir Conservation* **16**, 30–34.

Henry O, Feer F, Sabatier D (2000). Diet of the lowland tapir (*Tapirus terrestris* L.) in French Guiana. *Biotropica* **32**, 364–8.

Holden J, Yanuar A, Martyr D (2003). The Asian tapir in Kerinci Seblat National Park, Sumatra: evidence collected through photo-trapping. *Oryx* **37**, 34–40.

Hoppe K, Koch P (2007). Reconstructing the migration patterns of late Pleistocene mammals from northern Florida, USA. *Quaternary Research* **68**, 347–52.

Hulbert R (2005). Late Miocene *Tapirus* (Mammalia, Perissodactyla) from Florida, with description of a new species, *Tapirus webbi. Bulletin of the Florida Museum of Natural History* **45**, 465–94.

Janis C (1993). Tertiary mammal evolution in the context of changing climates, vegetation and tectonic events. *Annual Reviews on Ecology and Systematics* 24, 467–500.

Kinnaird M, Sanderson E, O'Brie T, Wibisono H, Wollmer G (2003). Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology* **17**, 245–57.

Lira Torres I, Naranjo EJ, Güiris E, Cruz-Aldán E (2004). Ecología de *Tapirus bairdii* (Perissodactyla: Tapiridae) en la Reserva de la Biosfera El Triunfo (Polígono I). *Acta Zoológica Mexicana* **20**, 1–21.

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- Lizcano DJ (2006). Ecology and conservation of large mammals in the Northern Andes (PhD dissertation). University of Kent, Canterbury, UK.
- Lizcano DJ, Cavelier J (2004). Características químicas de los salados y hábitos alimenticios de la danta de montaña (*Tapirus pinchaque* Roulin 1829) en los Andes centrales de Colombia. *Mastozoología Neotropical* **11**, 193–201.
- Lizcano DJ, Cavelier J (2000). Daily and seasonal activity of the mountain tapir (*Tapirus pinchaque*) in the Central Andes of Colombia. *Journal of Zoology* **252**, 429–35.
- Lizcano DJ, Cavelier J (2004). Using GPS collars to study mountain tapirs (*Tapirus pinchaque*) in the central Andes of Colombia. *Tapir Conservation* **13**, 18–23.
- Lizcano DJ, Pizarro V, Cavelier J, Camona J (2002). Geographic distribution and population size of mountain tapir (*Tapirus pinchaque*) in Colombia. *Journal of Biogeography* **28**, 1–9.
- MacFadden B (2000). Cenozoic mammalian herbivores from the Americas: reconstructing ancient diets and terrestrial communities. *Annual Reviews of Ecology and Systematics* **31**, 33–59.
- Medici EP (2010). Assessing the viability of lowland tapir populations in a fragmented landscape (PhD dissertation). University of Kent, Canterbury, UK.
- Medici EP (2011). Family Tapiridae (Tapirs). In: Wilson DE, Mittermeier RA, eds. *Handbook of the Mammals of the World, Volume 2: Hoofed Mammals*. Lynx Edicions, Spain, pp. 182–204.
- Medway L (1974). Food of a tapir, *Tapirus indicus*. Malayan Nature Journal **28**, 90–93.
- Montenegro OL (1998). The behavior of lowland tapir (*Tapirus terrestris*) at a natural mineral lick in the Peruvian Amazon (MSc thesis). University of Florida, Gainesville, FL.
- Naranjo EJ (1995a). Abundancia y uso de hábitat del tapir (*Tapirus bairdii*) en un bosque tropical húmedo de Costa Rica. *Vida Silvestre Neotropical* **4**, 20–31.
- Naranjo EJ (1995b). Hábitos de alimentación del tapir (*Tapirus bairdii*) en un bosque tropical húmedo de Costa Rica. *Vida Silvestre Neotropical* **4**, 32–7.
- Naranjo EJ (2009). Ecology and conservation of Baird's tapir in Mexico. *Tropical Conservation Science* **2**, 140–58.
- Naranjo EJ, Bodmer RE (2002). Population ecology and conservation of Baird's tapir (*Tapirus bairdii*) in the

Lacandon Forest, México. *Tapir Conservation* 11, 25–33.

- Naranjo EJ, Cruz-Aldán E (1998). Ecología del tapir en la Reserva de la Biósfera La Sepultura. *Acta Zoológica Mexicana* **73**, 111–25.
- Naranjo EJ, Vaughan C (2000). Ampliación del ámbito altitudinal del Tapir centroamericano (*Tapirus bair-dii*). *Revista de Biología Tropical* **48**, 724.
- Norman JE, Ashley MV (2000). Phylogenetics of Perissodactyla and test of the molecular clock. *Journal of Molecular Evolution* **50**, 11–21.
- Noss A, Cuellar R, Barrientos J *et al.* (2003). A camera trapping and radio telemetry study of lowland tapir (*Tapirus terrestris*) in Bolivian dry forest. *Tapir Conservation* **12**, 24–32.
- Novarino W, Karimah S, Jarulis N, Silmi M, Syafri M (2004). Habitat use by Malay tapir (*Tapirus indicus*) in West Sumatra, Indonesia. *Tapir Conservation* **13**, 14–8.
- Olmos F, Pardini R, Boulhosa R, Burgi R, Morsello C (1999). Do tapirs steal food from palm seed predators or give them a lift? *Biotropica* **31**, 375–9.
- Olmos O (1997). Tapirs as seed dispersers and predators. In: Brooks D, Bodmer RE, Matola S, eds. *Tapirs: Status Survey and Conservation Action Plan*. IUCN/SSC Tapir Specialist Group. IUCN, Gland, Switzerland, pp. 3–9.
- Padilla M, Dowler R (1994). *Tapirus terrestris. Mammalian Species* **481**, 1–8.
- Radinsky L (1965). A new genus of early eocene tapiroid (Mammalia, Perissodactyla). *Journal of Paleontology* **40**, 740–42.
- Salas L (1996). Habitat use by lowland tapirs (*Tapirus terrestris* L.) in the Tabaro river valley, southern Venezuela. *Canada Journal of Zoology* **74**, 1452–8.
- Salas L, Fuller T (1996). Diet of the lowland tapir (*Tapirus terrestris* L.) in Tabaro river valley, southern Venezuela. *Canada Journal of Zoology* **74**, 1444–51.
- Taber A, Chalukian S, Minkowski K *et al.* (2008). Range-wide status of lowland tapir (*Tapirus terrestris*) and white-lipped peccary (*Tayassu pecari*). Final report. Wildlife Conservation Society, Buenos Aires, Argentina.
- Talamoni S, Assis M (2009). Feeding habit of the Brazilian tapir, *Tapirus terrestris* (Perissodactyla: Tapiridae) in a vegetation transition zone in south-eastern Brazil. *Zoologia* 26, 251–4.

- Tejeda-Cruz C, Naranjo EJ, Cuarón AD, Perales H, Cruz-Burguete JL (2009). Habitat use of wild ungulates in fragmented landscapes of the Lacandon Forest, southern Mexico. *Mammalia* **73**, 211–9.
- Terwilliger V (1978). Natural history of Baird's tapir on Barro Colorado Island, Panama canal zone. *Biotropica* **10**, 211–20.
- Tobler M (2002). Habitat use and diet of Baird's tapir (*Tapirus bairdii*) in a montane cloud forest of the Cordillera de Talamanca, Costa Rica. *Biotropica* **34**, 468–74.
- Tobler M (2008). The ecology of the lowland tapir in Madre de Dios, Perú: using new technologies to study large rainforest mammals (PhD dissertation). Texas A&M University, College Station, TX, USA.
- Tófoli CF (2006). Frugivoria e dispersão de sementes por *Tapirus terrestris* (Linnaeus, 1758) na paisagem fragmentada do Pontal do Paranapanema, São Paulo

(MSc thesis). Universidade de São Paulo, São Paulo, Brazil.

- Tong H, Liu J, Han L (2002). On fossil remains of early pleistocene tapir (Perissodactyla, Mammalia) from Fachang, Anhui. *Chinese Science Bulletin* 47, 586– 90.
- Wiens J (1989). Spatial scaling in ecology. *Functional Ecology* **3**, 385–97.
- Williams KD (1980). Browse use, feeding behavior and management of the Malayan tapir. *Journal of Wildlife Management* 22, 489–94.
- Zollner P (2000). Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecology* **15**, 523–33.
- Zorzi BT (2009). Frugivoria por *Tapirus terrestris* em três regiões do Pantanal, Brasil (MSc thesis). Universidade Federal de Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul, Brazil.