

Rafael Reyna-Hurtado  
Colin A. Chapman *Editors*

# Movement Ecology of Neotropical Forest Mammals

Focus on Social Animals

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# Foreword

Félix Samuel Rodríguez de la Fuente (1928–1980) was a Spanish naturalist who made an outstanding impact on the global public through his radio and TV programs on wildlife and conservation. In the early 1970s, he led a group of Spanish biologists in an incredible project, the *Encyclopedia Salvat of the World Fauna* (later collated as “World of Wildlife” or “Fauna Mundial”), publishing a 24-page illustrated volume every week for 3 successive years. As an Israeli teenager eager to learn about wildlife and nature, I waited impatiently every Thursday morning for the next Hebrew-translated Wildlife volume sold in only one newsstand in the center of Eilat, my hometown. Every Wildlife volume brought wonderful stories and beautiful pictures to Eilat about all sorts of incredible creatures and landscapes from far away. As I am sure was the case for many other nature-lovers at my age, the Wildlife volumes dedicated to tropical regions captured my imagination more than anything else. Volumes 95–107 focused on the neotropics, describing and explaining their diverse faunas and citing Marston Bates as labeling neotropical animals as the most bizarre creatures on Earth. Volumes 102 and 103 vividly described the primates and carnivores of the neotropics, highlighting their locomotion skills, social grouping, hunting tactics, and territorial behavior. The curiosity that the Wildlife neotropic volumes instilled in a teenaged nature-lover in the desert town of Eilat is perhaps best understood when considering the so-called naïve drawings of jungle scenes by Henri Rousseau, famous for fiercely delivering the fantasy of the wild tropics despite never leaving France.

More than four decades have passed since I first read about the life of neotropical animals on the move in the Wildlife encyclopedia. Unlike Rousseau, I have been fortunate enough to witness neotropical animals moving throughout their natural habitats in Panama, Peru, and Brazil. My childhood fascination for wildlife on the move has meanwhile matured into a profession called *movement ecology*. Movement of organisms, the subject of this book, characterizes all species, affects individual fitness, determines evolutionary pathways, and shapes ecological processes, including the most stressful global environmental problems and conservation concerns we face today. The movement ecology framework offers a conceptual platform for guiding and uniting research on movement of organisms by delineating the basic

mechanistic components common to all types of movement and all kinds of organisms. Beyond the theoretical integration, movement ecology has experienced rapid progress over the last decade thanks to technological advancements allowing accurate tracking of wildlife by GPS and other tracking technologies, as well as advanced data analysis tools. In this book, Rafael Reyna-Hurtado, Colin A. Chapman, and their colleagues aimed to illustrate the importance of movement ecology research on neotropical mammals to achieve a better understanding of key ecological processes for advancing effective conservation efforts in these hyperdiverse yet fragile and endangered tropical ecosystems.

This book includes 3 useful introductory/review/concluding chapters and 12 research chapters describing studies of 9 different mammalian species from 4 different orders and 6 families. Common to all research chapters is the focus on the effects of various external factors – including hurricanes, hunters, landscape structure, food resources, seasonality, and topography – on the movement paths of individual animals quantified by direct observational tracking, VHF collars, and mostly GPS devices. External factors and movement paths are two of the five basic components of the movement ecology framework; the three other components – internal state (determining why to move), motion capacity (determining how to move), and navigation capacity (determining when and where to move) – describe the key features of the focal individual that likely interact with the external factors and with each other to jointly shape the resulting movement path. Reported associations between external factors and movement path, with some insights about the internal state, include, for example, the longer travel distances (movement path) of fawning female (internal state) white-tailed deer during the hot dry season (external factor) compared to the flooding season (Chap. 8). Additionally, fruit availability (external factor) did not affect group cohesion (external effect on the internal state) and daily travel distance (movement path) among four groups of woolly monkeys, but mating opportunities (external factor) significantly increased daily travel distance, suggesting that spatial dynamics in these groups are governed by competition over mates rather than food (Chap. 10). Furthermore, male (internal state) jaguars covered twice as much area compared to females, and one female (internal state) jaguar favored a relatively small patch of rugged forested terrain (external factor), presumably to provide a refuge while rearing cubs (Chap. 13).

Insights into the other two basic components of movement ecology that could further elucidate the mechanisms underlying variation in movement paths were usually not estimated directly due to data limitations (further discussed below) but were demonstrated or suggested in some studies. For example, larger groups of howler monkeys tended to move over extended areas and more frequently moved toward isolated trees in a fragmented landscape by walking on the ground; such “terrestrial locomotion,” a rather unusual mode of motion for this canopy-dwelling species, occurred mostly in the rainy season and was initiated mostly by the oldest male in one group and an adult female carrying an infant in another (external and internal effects on motion capacity) (Chap. 9). Furthermore, the tendency toward more restricted movements of two GPS-tracked Baird’s tapirs after hurricane Otto was suggested to reflect either higher food availability (external effects on the internal state),

difficulty in moving in a complex terrain further induced by fallen trees (external effects on motion capacity), or lower visibility due to enhanced growth in canopy gaps (external effects on navigation capacity) (Chap. 2).

The immense use of GPS devices by humans has greatly facilitated the development of GPS devices for wildlife tracking, arguably constituting the most important technological development thus far in movement ecology research. GPS devices have been applied mostly to track mammals and birds of relatively large (>100 g) body mass, including many mammalian species studied in this collection. As illustrated for Colombian woolly monkeys (Chap. 11), GPS tracking could be advantageous over direct observations in estimating movement and home range due to difficulties in directly tracking monkey groups in areas of steep topography and across inaccessible landscape features. Direct tracking, though, can be advantageous by providing behavioral and ecological data not easily available by GPS. Other limitations of GPS tracking reported in various chapters occur due to problems in data download via satellites in closed canopy habitats and complex terrain, failure of tag drop-off mechanisms, and nearly inaccessible areas necessitating tremendous efforts to recover deployed data loggers. Overall, I congratulate the authors for all of these incredible efforts and their determination to pursue their goals, proven compulsory for making this book possible. In addition, many chapters in this book have applied novel data analysis tools such as the semivariance approach capable of accommodating irregularly sampled data (Chap. 6), the biased random bridge, and a step selection function (Chap. 13). It is worth stressing that problems resulting from data limitations were not neglected in these studies; on the contrary, the authors have carefully interpreted their results, highlighted small sample size and/or other data-related uncertainties, and repeatedly emphasized that further insights about their systems and research questions should be pursued by obtaining richer data sets through more effective tracking devices and data download procedures. Auxiliary data on energy expenditure, behavior, and environmental factors might also be obtained in future studies through other bio-logging technologies including accelerometers and various other sensors, to further enrich our ability to quantify the internal state, motion and navigation constraints, and behavioral response to the variable external environment the animal encounters en route.

In summary, I warmly congratulate this excellent team of authors for covering a wide range of topics, questions, species, and ecosystems and for proving that insightful movement ecology research is feasible even in such challenging environments and under very difficult working conditions. I am confident that the important research projects presented in this book will prove critical for further advancement of the study of animal movement ecology in the neotropics and in other challenging environments to ensure that threatened wildlife will prevail.

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# Chapter 1

## Why Movement Ecology Matters



Colin A. Chapman and Rafael Reyna-Hurtado

The scientific discipline of “Movement Ecology” (Nathan et al. 2008) has played an important role in advancing our understanding of almost every ecological and evolutionary process, from nutrient cycling, to habitat selection, to population dynamics and community ecology. Interestingly, it has been almost a quarter of a century ago since Rodgers and Anson (1994) stated that GPS-based animal-location systems would become the standard for habitat selection studies. They were right! The data made available from GPS telemetry (i.e., sequence of GPS locations) quickly boosted the field of “Movement Ecology” (Nathan et al. 2008), and this field was also greatly advanced when the Max Planck Institute of Ornithology developed a free online database, Movebank ([movebank.org](http://movebank.org)), that allowed movement data from many, many species to be freely accessed and analysed (millions and millions of travel routes). Further advancements became possible with the development and use of new analytical tools to understand the rules used by the study animals to move (Ropert-Coudert and Wilson 2005; Sengupta et al. 2018).

In 2008 a Special Feature of the Proceedings of the National Academy of Science was published that was based on an international project held at the Institute for Advanced Studies in Israel. The Special Feature aimed to generate a conceptual

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framework of movement and of ways of generating and analysing movement paths (Nathan 2008; Nathan et al. 2008). In addition, the Special Feature illustrated the application of the framework to different types of questions and illustrated the scope of the Movement Ecology field, both from theoretical and taxonomic perspectives (Fryxell et al. 2008; Holyoak et al. 2008).

The study of animal movement progressively has become more important as the world has become more and more aware of how human actions were endangering natural systems. Today, the loss of tropical forest is causing the extinction and endangerment of many species (Estrada et al. 2017; Pimm et al. 2014). Globally, it is estimated that biodiversity is being lost at an accelerating rate, with current extinction rates approximately 1000 times higher than background rates (Pimm et al. 2014). Recent estimates suggest that 11,000–58,000 species are lost each year and that surviving vertebrate species have declined in abundance by 25% since 1970 (Dirzo et al. 2014). Humans are clearly responsible for this accelerating loss of biodiversity, particularly in the neotropics. Between 2000 and 2012, 2.3 million km<sup>2</sup> of forest was lost globally, and in the tropics forest, loss increased each year (Hansen et al. 2013). To put this in perspective, this area is approximately the size of Mexico. Global estimates of the extent of wildlife over-exploitation are very poor. However, Bennett et al. (2000) estimated that six million mammals were hunted annually in Malaysian Borneo. With respect to climate change, temperatures are predicted to increase by 1.5 °C by the end of the twenty-first century (IPCC 2014), and using moderate greenhouse gas emission estimates, it is projected that by 2100 75% of all tropical forests present in 2000 will experience temperatures that are higher than the temperatures presently supporting closed canopy forests (Peres et al. 2016; Wright et al. 2009).

This volume represents the culmination of a discussion that started at our field site 4 years ago. We were both adamant that a greater understanding of animal movement would advance tropical conservation efforts, and we were determined to illustrate this. As a result, we gathered together an amazing group of scholars who worked on animal movement and had them contribute papers to this book. We sincerely hope that when readers finish examining the contributions we have gathered together, they will be convinced of the importance of “Movement Ecology” advancing a myriad of academic questions and addressing many of the most important conservation/management questions. Most importantly, we hope that the chapters in this volume inspire the next generation to devote the huge amounts of time to collect and analyse animal movement data to conserve the amazing mammals that we find in the neotropics.

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# Chapter 2

## The Impact of Hurricane Otto on Baird's Tapir Movement in Nicaragua's Indio Maíz Biological Reserve



Christopher A. Jordan, Brendan Hoover, Armando J. Dans, Cody Schank, and Jennifer A. Miller

### 2.1 Introduction

Hurricanes have played an important role in the successional pathways of Nicaragua's Caribbean Coast forests throughout history. Records show that between 1892 and 1996, Nicaragua was hit by 40 tropical cyclones, 18 of which made land-fall as hurricanes (Centro Humboldt and Fundación del Río 2017). The Category 5 Hurricane Joan that battered Nicaragua in 1989 is perhaps the country's best known hurricane due to the damage it brought on south Caribbean Coast communities and cities and to the extensive research carried out after the hurricane to document the regeneration of the region's lowland tropical forests (Yih et al. 1991). While post-hurricane forest regeneration has been studied comprehensively, the impact of hurricanes on wildlife is comparatively unknown. The few studies that exist address how rapidly certain species assemblages recover over time (Will 1991). Yet the drastic changes in habitat structure and resource availability caused by hurricanes affect not only the species richness of the forest but also the behavior and movement ecology of species, which could have implications for species' carrying capacities, survival rates, and reproduction in sites damaged by hurricanes. For example, in some forests affected by Hurricane Joan, only 27% of trees remained standing and

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only 18% of trees had leaves in the immediate aftermath of the storm. For primates, this almost certainly shifted their general foraging patterns and habitat use. For large mammals such as jaguars (*Panthera onca*) and Baird's tapirs (*Tapirus bairdii*), the 73% of trees that fell during Hurricane Joan must have turned the forest floor into a messy labyrinth of fallen trees and limbs that affected their ability to move efficiently and thus forced them to adjust their hunting and browsing strategies, respectively (Yih et al. 1991). While it is difficult to collect data on animal movements before and after hurricanes due to the unpredictable nature of the storms, these data are critical to understanding how hurricanes affect animal movement and ultimately their capacity to thrive in hurricane-damaged forests.

Understanding the full impact of hurricanes on neotropical forest wildlife is even more critical considering recent studies that indicate rising sea surface temperatures in the Western Caribbean are expected to produce larger cyclones with higher intensity throughout the region (Baldini et al. 2016; Overland et al. 2016). In effect, this means that in the remainder of this century, the Western Caribbean is likely to see more intense storms capable of damaging more extensive areas of forest.

In this chapter, we report on a unique dataset collected with GPS collars that were installed on two Baird's tapirs before the Category 2–3 Hurricane Otto in Nicaragua's Indio Maíz Biological Reserve during 2016. These data gave us the opportunity to examine how hurricane damage to these tapirs' home ranges affected their movement, which in turn gives us insight into how hurricanes and similar extreme weather events may affect the survival of this globally endangered large mammal in the current century. We hypothesized that tapir home ranges would decrease in size due to the increased energy required for individual tapirs to move long distances in hurricane-damaged forest, in addition to an increase in food density and availability on the forest floor due to post-hurricane forest recovery. We also expected the data to show that tapirs would avoid areas with the combination of large slopes and many downed trees due to the energy required to move around these areas. Likewise, given that rivers and streams post-hurricane are relatively open areas compared with the damaged forest, we hypothesized that tapirs might be using rivers and streams simply because they offer an efficient means of moving around their home ranges.

## 2.2 Study Site

The 2639 km<sup>2</sup> Indio Maíz Biological Reserve in southeastern Nicaragua constitutes important habitat for a host of regionally endangered and threatened species, such as Baird's tapirs, jaguars, and white-lipped peccaries (*Tayassu pecari*), great green macaws (*Ara ambiguus*), and wild almond trees (*Dipteryx panamensis*) (Fig. 2.1). The reserve receives more than 4000 mm of annual rainfall and is comprised of lowland tropical rainforest, *Raphia* palm swamps, and seasonally flooded forests, and the lower reaches of its rivers harbor freshwater grasses that sustain local manatee (*Trichechus manatus*) populations. The reserve has no road access; its heart is only accessible by boat or dugout canoe. Indio Maíz is a core area of the over 4000 km<sup>2</sup> terrestrial portion of the Rama-Kriol indigenous territory and is inhabited



**Fig. 2.1** Path of 2016's Hurricane Otto through the Indio Maíz Biological Reserve in the southeast corner of Nicaragua

by Rama indigenous peoples, afro-descendant Kriol, and, increasingly, illegal cattle ranchers but continues to have an extremely low human density.

Historically Indio Maíz has been Nicaragua's best-preserved rainforest and was comprised almost entirely of primary forest (Fig. 2.2). Before 2016 there was no known historical record of Indio Maíz having been affected by a hurricane (Centro Humboldt and Fundación del Río 2017). Indio Maíz is one of the five largest forests





**Fig. 2.2** A photo of the primary forest of Indio Maíz in 2015, long before Hurricane Otto

remaining in Central America and also one of the most important core areas remaining for the conservation of the globally endangered Baird's tapir (Schank et al. 2017). Nonetheless, Nicaragua has one of the highest rates of forest loss in Central America (Hansen et al. 2013), and government agencies responsible for managing protected areas are under-resourced and understaffed and do not have the political mandate to protect the country's forests. This is even true in Indio Maíz, which is the protected area with the strictest environmental regulations in the entire country.

### 2.3 Study Species

Baird's tapirs are members of the order Perissodactyla, or odd-toed ungulates, making them evolutionary relatives of the horse and the rhinoceros. The species is the largest terrestrial mammal in the neotropics, and tapirs are one of the most ecologically important species in the forested landscapes they inhabit (Peres et al. 2016). Tapirs have large daily food requirements and are prodigious browsers, consuming leaves, seeds, and fruits from an estimated 100–200 different species of plants (Jordan, unpublished data). Through their selective browsing behavior and dispersal of seeds through their feces, they have a large impact on the successional pathways of neotropical forests, and for this reason we often refer to them as the “farmers of the forest” and “ecosystem engineers” (O’Farrill et al. 2013).

There have been few studies on Baird's tapir movement. The most frequently cited study is from Corcovado National Park (Costa Rica) where radio telemetry data collected over the course of approximately 1 year on five adults (three females and two males) were used to estimate a mean home range size of only 1.25 km<sup>2</sup> for all tapirs combined using 95% minimum convex polygon (MCP) (Foerster and Vaughan 2002). A more recent study provided much larger estimates ranging from 4.1 to 39.9 km<sup>2</sup>, but the dataset differs markedly from our study in that mostly camera-trap data were used to estimate home range size rather than telemetry data (Reyna-Hurtado et al. 2016).

The Baird's tapir is classified as globally endangered by the IUCN (García et al. 2016). Experts estimate that the current global population could have as few as 4500 mature adults (García et al. 2016). The main threats to the survival of the species include extensive deforestation, unsustainable poaching, and climate change (García et al. 2016). Tapirs are solitary animals with large spatial requirements and a slow reproductive cycle given their gestation period of approximately 400 days (Brooks et al. 1997; García et al. 2016). Massive forest loss across most of Central America in the last 15 years combined with significant hunting has diminished the global Baird's tapir population by more than 50% in the past three generations and left the remaining tapirs in mostly isolated subpopulations, many of which may not be genetically viable (García et al. 2016; Hansen et al. 2013; Jordan et al. 2014). In the Selva Maya, the species' northernmost stronghold and one of its most important core habitats, there is concern that climate change may decrease water availability and decrease the suitability of the habitat for tapirs over the course of this century (O'Farrill et al. 2014). Without a long-term, large-scale effort to reverse recent trends in the species' populations, Baird's tapirs are vulnerable to becoming critically endangered (García et al. 2016). In this context, the potential for hurricanes to negatively affect Baird's tapirs' survival and carrying capacity in important core areas like the Indio Maíz Biological Reserve could further threaten the survival of the species.

## 2.4 Hurricane Otto

Hurricane Otto was an unusually late-forming hurricane during 2016's hurricane season. The storm first achieved hurricane status on November 23, 2016 approximately 240 km from the Nicaraguan/Costa Rican border (Brown 2017). Hurricane Otto made landfall as a Category 3 storm with sustained winds of approximately 175 km/h on November 24, 2016 near Greytown in the southeastern corner of Nicaragua and then began its path across the Indio Maíz Biological Reserve (Brown 2017).

Hurricane Otto was a relatively small storm, with hurricane force winds extending only 16–32 km from the center of the storm (Brown 2017). Although the storm lost strength fairly quickly as it moved across Indio Maíz, the eye of Otto remained intact across almost the entirety of the Central American isthmus and caused extensive damage to reserve's primary forest (Centro Humboldt and Fundación del Río



**Fig. 2.3** A photo of Cucaracha Hill in the Indio Maíz Biological Reserve approximately 1 week after Hurricane Otto passed through Indio Maíz. Before the hurricane, this hill was covered with primary forest. (Photo courtesy of Camilo de Castro)

2017) (Fig. 2.3). For instance, in seven sites surveyed in the immediate aftermath of the hurricane, 72.7% of trees had fallen to the forest floor (Centro Humboldt and Fundación del Río 2017). Local researchers estimated that Hurricane Otto damaged 1667.9 km<sup>2</sup> of forest in Indio Maíz (Centro Humboldt and Fundación del Río 2017).

## 2.5 Data and Methodology

### 2.5.1 *Tapir Captures*

Our team captured and immobilized Baird's tapirs as a part of a GPS telemetry project during two separate capture expeditions in 2016, the first from March 29 to May 8 and the second from August 5 to 24. During both expeditions, our team used pitfall traps camouflaged with leaf litter and dirt to capture tapirs.

We built 18 traps during the first expedition then monitored them over a period of 35 days. Total effort was 385 trap nights during the first expedition during which we captured two adult male tapirs and one adult female tapir (0.0078 capture rate). The female's collar was not fitted properly and fell off after a few days.

We built 12 traps during the second expedition, but only monitored them for 9 days due to unexpected torrential rains that forced our team to end the expedition early. Total effort was 75 trap nights. During this expedition we captured one adult male Wes (0.013 capture rate). No nontarget species were captured in pitfalls during either expedition with the exception of a single Tome's spiny rat (*Proechimys semi-spinosus*) that we removed from the trap and released.

All captured tapirs were immobilized and then fitted with a Telonics Iridium collar programmed to attempt a GPS fix of the animal's location every hour and to make periodic satellite transmissions. All collars had automatic release mechanisms programmed to release approximately 1 year after collar installation; however the automatic release mechanisms malfunctioned and did not drop off. After multiple and ongoing expeditions to recapture collared individuals and recover the information stored on board, we managed to recapture one of the males collared in April 2016 (Almuk) and the male (Wes) captured in August 2016. Expeditions continue to capture the final individual.

Almuk was captured and collared on April 8, 2016. From this date the collar continued to attempt GPS fixes every hour until September 7, 2017. During this interval, Almuk's collar successfully recorded a total of 8830 locations, including 4217 before the hurricane and 4613 after the hurricane. Almuk's collar had an overall fix acquisition rate of 70.6%.

Wes was captured and collared on August 16, 2016 with hourly GPS fixes attempted until January 23, 2018. During this interval, a total of 8532 locations were recorded, including 1464 before the hurricane and 7068 after the hurricane. Wes' collar had an overall fix acquisition rate of 64.8%.

## 2.5.2 Data Analysis

We investigated the relationship of tapir movement with slope and distance to streams and rivers to test our hypothesis that tapirs would utilize areas of the forest that maximized the efficiency of their movements, such as along waterways and in areas with lower slopes. We digitized all visible streams and rivers from topographic maps (US National Imagery and Mapping Agency, Series E751) and calculated the distance from GPS fixes to these waterways (units = meters). We then compared these samples before and after the hurricane. We also downloaded a 30-m DEM (Tachikawa et al. 2011), calculated slope (units = degrees), and did another comparison of before and after values. This was done to determine how tapir movement changed in relation to these environmental variables.

To analyze tapir movement patterns in general, we compared the size of home ranges before and after the hurricane. We used a fixed kernel density estimation (KDE) (Worton 1989; Seaman and Powell 1996) to calculate the 95% (home range) and 50% (core area) utilization distributions for each tapir before and after the hurricane. To smooth the data, we used the default smoothing factor, which is generated for each of the trajectory datasets (Worton 1995). Smoothing is beneficial because it reduces variance in the low sample areas and reduces bias in areas with many obser-

vations (Worton 1989). Home range estimators like KDE potentially misrepresent home ranges because they treat movement data, which is inherently spatially and temporally autocorrelated, as a point pattern rather than as a movement process (Hemson et al. 2005). Autocorrelation can be reduced by filtering points so they are statistically independent (Welch et al. 2015); however, the spatiotemporal autocorrelation can also emerge as a function of an animal’s preference for specific areas within their home range. Therefore, instead of filtering data, we used time local convex hull (T-LoCoH) which is a time-scaled home range estimator (Lyons et al. 2013), in addition to KDE. T-LoCoH converts the time difference between point pairs into a time-scaled distance metric used with spatial proximity to construct nearest neighbor convex hulls (Lyons et al. 2013). A scaling factor,  $s$ , determines the maximum amount of time from which a spatial neighbor is still considered correlated to the focal location and is therefore calculated as a nearest neighbor (Lyons et al. 2013). As the scaling factor,  $s$ , increases, the time factor is weighted more heavily;  $s = 0$  means time is not considered at all. To determine our  $s$  factor, we plotted our data to see the natural frequencies in the data for the distance of each point to the centroid of the entire datasets over time (Lyons 2014). Using that technique, we set used  $s = 0.015$ . We then compared the areas calculated using both KDE and T-LoCoH before and after the hurricane to determine if change had occurred. Finally, we also investigated how movement velocity changed before and after the hurricane, calculated as the distance between subsequent GPS fixes, divided by the time elapsed between them.

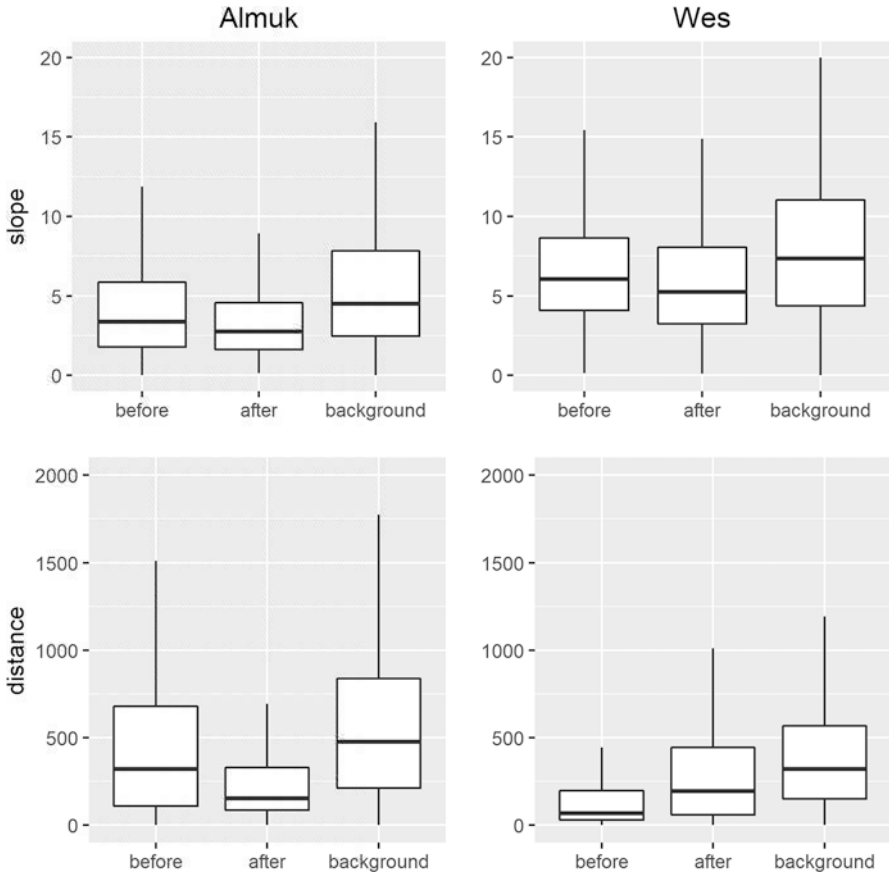
## 2.6 Results

Welch’s t-test results between samples of environmental variables (slope and distance to waterways) for GPS fixes before and after the hurricane show that (1) both individuals used areas with lower slopes after the hurricane and (2) Wes used habitat farther from rivers with a higher frequency after the hurricane, whereas Almuk used habitat closer from rivers with a higher frequency after the hurricane (Table 2.1, Fig. 2.4). During recent recapture expeditions for Wes, however, we noted that there were several small creeks in the areas far from the main river that he appeared to frequent. These small creeks were not included in our rivers and streams layer, so

**Table 2.1** Comparison, using Welch’s t-test, between samples of environmental variables for GPS fixes before and after the hurricane (negative values in the confidence intervals indicate higher values after the hurricane)

	Individual	Mean before	Mean after	95% Conf. intervals for difference of means (before–after)
Slope	Almuk	4.22	3.59	0.499–0.772
	Wes	6.81	5.86	0.713–1.187
Distance to waterways	Almuk	426	287	124–153
	Wes	134	278	–154 to –134

All differences were statistically significant at  $p < 0.001$



**Fig. 2.4** Boxplots for the comparison between slope and distance to waterways for GPS fixes before and after the hurricane. “Background” represents all of the values in the study area – the extent that includes a buffer of 3 km from all GPS points for each individual. Outliers have been removed

there is the chance that our analyses were unable to capture the true relationship between Wes’ movements and local waterways.

Given that our data for Wes only included approximately 3 months pre-hurricane and 14 months post-hurricane, we do not believe that his pre-hurricane data were enough to capture his entire home range. For this reason, we restricted our comparisons pre- and post-hurricane to the area of overlap between his pre-hurricane and post-hurricane home ranges. Therefore, results for Wes do not represent his entire home range but rather his home range use within this area of overlap. In all analyses, Wes’ use of this area of home range decreased significantly after the hurricane (Table 2.2). However we also provide estimates for Wes’ full post-hurricane dataset as this likely does represent his full home range after the storm (Table 2.2). In contrast to Wes, Almuk’s dataset included a relatively equal number of points both pre- and

**Table 2.2** Comparison of home range (95% isopleth) and core areas (50% isopleth) of Wes before–after Hurricane Otto using both KDE and T-LoCoH

Tapir2 (Wes)	Pre-hurricane area (km <sup>2</sup> )	Post-hurricane area of overlap (km <sup>2</sup> )	Full post-hurricane dataset (km <sup>2</sup> )
MCP (Home range)	18.32	9.61	11.90
T-LoCoH (Home range)	4.21	0.87	1.24
T-LoCoH (Core area)	0.35	0.09	0.11
KDE (Home range)	14.99	2.85	4.50
KDE (Core area)	1.96	0.51	0.82

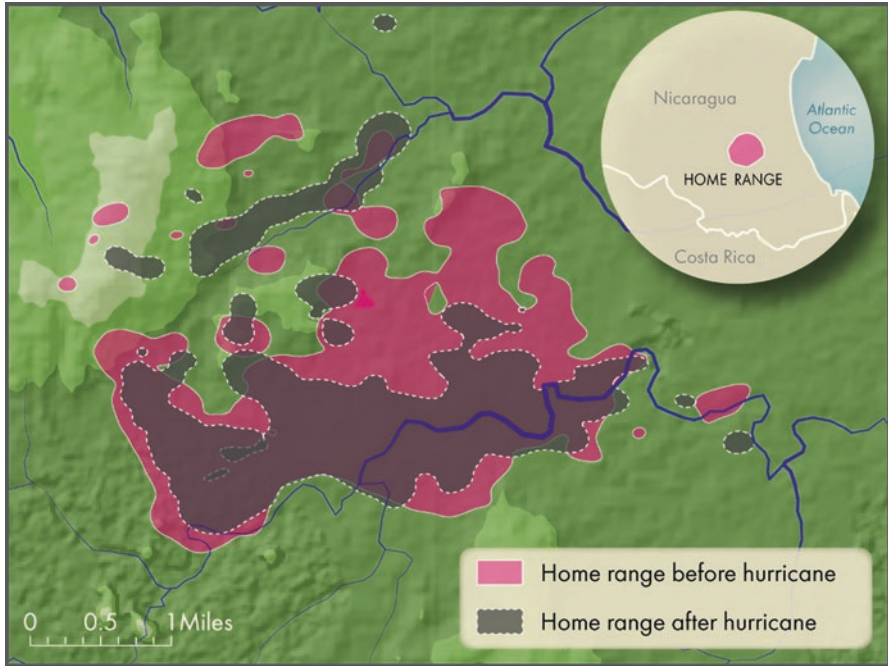
**Table 2.3** Comparison of home range and core areas of Almuk before and after Hurricane Otto using MCP, KDE, and T-LoCoH

Tapir 1 (Almuk)	Pre-hurricane area (km <sup>2</sup> )	Post-hurricane area (km <sup>2</sup> )
MCP (Home range)	18.72	16.12
T-LoCoH (Home range)	11.25	3.35
T-LoCoH (Core area)	0.78	0.13
KDE (Home range)	13.57	8.73
KDE (Core area)	1.99	1.22

post-hurricane, and thus his entire dataset was used in the analyses. Similar to Wes, all estimates of Almuk’s home range decreased significantly post-hurricane (Table 2.3, Fig. 2.5). Finally, Almuk’s velocity pre-hurricane was 1.17 m/s, which decreased by 67–0.39 m/s post-hurricane, while Wes’ velocity pre-hurricane was 0.42 m/s and decreased slightly to 0.40 m/s post-hurricane.

## 2.7 Discussion

The home range estimates for these two tapirs are interesting given that the estimates from the most commonly cited paper on Baird’s tapir home ranges collected from animals in Corcovado National Park (Costa Rica) range from 0.968 to 1.25 km<sup>2</sup> using 95% minimum convex polygon (MCP) (Foerster and Vaughan 2002). According to our estimates at 95% isopleth, in the primary forest of Indio Maíz before the hurricane, the two tapirs reported on in this chapter had home ranges that measured an order of magnitude more than what was previously reported. For example, using KDE (95% isopleth) which is a traditional, non-time-bound method that can be used for historical comparisons, Almuk had a home range of 13.57 km<sup>2</sup> and Wes 14.99 km<sup>2</sup>. Using MCP, pre-hurricane estimates for their home ranges are 18.72 km<sup>2</sup> and 18.32 km<sup>2</sup>, respectively. Even in the hurricane-damaged forest, which we assume is similar to secondary forest, home ranges are still larger than those reported in Corcovado, although similar to those reported by Reyna-Hurtado et al. (2016).



**Fig. 2.5** KDE home range results pre- and post-hurricane for Almuk . The pre- and post-hurricane home range results for Wes are not included in this figure because we are unsure if the pre-hurricane data was sufficient for capturing his entire home range

Using MCP with post-hurricane data, our estimates for their home ranges were 16.12 km<sup>2</sup> and 11.90 km<sup>2</sup>, respectively. In the case of Wes, these estimates are particularly interesting because we are not confident that his pre-hurricane home range represents his entire home range given that we only collected data on him for 3 months before the storm. Importantly, the pre-hurricane home ranges are consistent with other adult tapirs that we have captured and collared in Indio Maíz. Thus, these new estimates for Baird's tapir home range are significant in that they show that the most frequently referenced estimates for the species are not consistent across the species' entire distribution. This, along with the fact that home ranges for the same individuals in the same locations changed along with significant changes in the condition of the forest, suggests that a home range estimate from one location cannot be extrapolated and used to estimate population size or density for Baird's tapirs in other sites throughout the species' global distribution.

Previous research has shown that Baird's tapirs prefer secondary forest over primary forest due to the greater availability of vegetation close to the forest floor (Foerster and Vaughan 2002; Fragoso 1983). Thus, tapirs are likely to have smaller home ranges in secondary forest, as they have to move less to consume the same amount of food. We predicted smaller home ranges post-hurricane considering that tree fall caused by Hurricane Otto triggered a massive release of nutrients on the forest floor which resulted in extremely rapid regeneration and therefore a spike in





**Fig. 2.6** Cucaracha Hill (the same hill pictured in Fig. 2.2) approximately 1 year after Hurricane Otto. (Photo courtesy of Camilo de Castro)

tapir food availability (Fig. 2.6). Furthermore, we optimistically predicted that in the short term, this might even increase the carrying capacity for Indio Maíz's tapirs and thus results in a larger population. Our results showed that there was a significant decrease in both of our collared tapirs' home ranges post-hurricane.

However, a look at the individual movement patterns in relation to slope and distance to streams and rivers puts our prediction of a subsequent increase in population into question. For instance, in the case of AlmuK, movements post-hurricane occurred close to rivers and streams and in areas with more gentle slopes than pre-hurricane, most likely in an attempt to move more efficiently around his home range. Anecdotally, increased difficulty of moving in the study area was observed by our field team, who estimated that walking the same distance can take five to six times longer post-hurricane simply because one has to constantly climb over and under a mess of fallen trees and limbs. This has been exacerbated even further as the forest regenerates because new growth has filled the gaps in the fallen trees and reduced visibility to almost nothing (this also increased the difficulty of recapturing AlmuK and Wes). Therefore following rivers and streams as much as possible because they tend to provide clearer paths allowed for more efficient and faster movement in general. While tapirs are certainly more adept at moving through the forest than our field team, it seems plausible that tapirs would do the same and look for the most efficient way to travel around their home ranges, and this is consistent with research on other species (Shepard et al. 2013; Wall et al. 2006). We hypothesized that optimizing efficiency would include concentrating movements: (a) along rivers and streams and/or (b) in lowland areas that do not cross hills of significant size covered in hurricane-damaged hardwood forest but rather stick to lowland areas (i.e., areas of lower slope) that likely have more palms and potentially less woody debris covering the forest floor. Our results support this hypothesis. Therefore, while tapirs do appear to have reduced home ranges in

Indio Maíz, we are unable to unequivocally conclude that this will lead to an increase in carrying capacity in the reserve. This is because our data suggest that AlmuK's and Wes' home ranges do not appear to have reduced solely due to an increase in food availability, but also because tapirs are selecting habitat that allows them to move efficiently. It is unclear if tapirs can now use the entirety of the landscape of Indio Maíz, such as the forested hills away from rivers and streams post-hurricane, and thus more research is needed to determine if the reduction in home range size will result in an increase in carrying capacity. It is also unclear if the restrictions on movement post-hurricane influences the dispersal capabilities of juveniles and/or the genetic connectivity of tapirs within Indio Maíz, but given our findings this is possible.

In addition to results on home ranges and habitat use, velocity post-hurricane was lower than pre-hurricane for both tapirs, with a more substantial decrease in the case of AlmuK. This is likely due to the combination of higher food availability on the forest floor resulting in less movement for foraging overall and the increased difficulty of moving around the forest due to fallen trees. We assume that there was a smaller decrease in Wes' velocity because his home range, while drastically altered by the hurricane, was visibly less damaged than AlmuK's. Future research should include using state-space models to differentiate behavioral modes like foraging and general movement before and after the hurricane to assess the significance of this decrease in velocity (Patterson et al. 2008).

Although two individuals represent a very small sample size for more robust movement pattern analyses, the unique nature of our dataset have allowed us a novel look into the immediate impact of hurricanes on the movement of Baird's tapirs. In the coming years as climate change produces stronger hurricanes capable of causing more extensive damage to the lowland forests of the Western Caribbean, it will be important to continue to monitor these and other tapirs in Indio Maíz to observe how Baird's tapirs home ranges change along with the regeneration of Indio Maíz's forests in order to better understand the long-term impacts of these storms.

This chapter shows that research on tapir movement is crucial to understanding changes in tapir behavior and movement when faced with natural perturbations to their habitat such as the damage caused by hurricanes. It also suggests that data on movement ecology of endangered species in fragmented, degraded, or damaged habitat are essential to understanding how these species survive outside of core areas of primary forest (Welch et al. 2015; Whittington et al. 2005). Such data will allow us to develop more effective and appropriate conservation plans for endangered species that are subject to human and/or natural perturbations.

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