

# Description of the movement of the Endangered Chaco Tortoise *Chelonoidis chilensis*

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Abstract.—The Chaco Tortoise Chelonoidis chilensis is the southernmost species of land tortoise in the world. This species is currently listed as Endangered not only due to habitat reduction and destruction, but also because of its value in the illegal pet trade. As both a grazer and a seed disperser, it serves as a keystone species in the dry ecosystems it inhabits. Despite its endangered status and important ecological role, there is currently limited information on the movement patterns of C. chilensis. In this work, we investigated the movement characteristics of this species over two seasons and in both sexes, using three complementary tracking techniques of spool-and-line, radiotelemetry, and GPS-based tracking, including the use of a device designed and developed by our team. To capture the most comprehensive view of movement patterns, each of the techniques used provides distinct strengths in characterizing spatial or temporal aspects of movement. We studied the movements of the tortoises over two seasons (spring 2020 and summer 2021), in their natural habitat near the city of San Antonio Oeste, Río Negro, Argentina. We tracked seven individuals (four males and three females) with the spool-and-line technique, 12 (six males and six females) with radiotelemetry, and 10 (four males and six females) with the GPS-based system. We estimated their daily home range (DHR) and speed of movement, measured the tortuosity of the walks and characterized their mean square displacement. The results indicated that C. chilensis remains within a DHR of 864 ± 283 m<sup>2</sup> in the spring season and 1034 ± 298 m<sup>2</sup> in the summer season. The most probable value of their velocity is 0.4 ± 0.1 m/min, with a median value of 0.6 ± 0.1 m/min, and the walks are characterized by bouts of foraging during movement, with periods of time spent exploring new spaces while also maintaining activity within their home ranges. Notably, we observed that C. chilensis can travel as much as 400 m in one day. The complementarity of our monitoring techniques allowed us to study and characterize the movement of this species at different scales. For example, the high spatial resolution of the spool-and-line technique can describe tortuosity, while the GPS-based and radiotelemetry techniques can describe trajectories with fine temporal resolution. To better understand how these animals move, the distances they can travel daily, and how these results depend on the season are relevant for making conservation decisions, while considering the significant impact that habitat fragmentation and other factors can have on their environment.

**Keywords.** GPS positioning, habitat use, radiotelemetry technique, spool-and-line technique, terrestrial tortoises

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# Introduction

Most animal species can execute complex movement patterns that generally depend on the environment, the intrinsic factors of individuals, and interactions with other individuals (Morales et al. 2005, 2010; Nathan 2008; Smouse et al. 2010). The complexity of these movements is reflected in their trajectories. In the case of foraging animals, these trajectories depend strongly on the vegetation, which largely determines their movement patterns. Thus, the dynamics of the vegetation community are closely linked to foraging, pollination, and seed dispersal, creating a mutualistic relationship with the animals that generally perform these tasks (Morales and Carlo 2006).

The foraging activity of animals is an active field of study aimed at identifying the optimal strategy under different hypotheses of animal perception and memory (Bartumeus et al. 2002; Barton et al. 2009; Fronhofer et al. 2013). There is considerable interest in the search strategies employed by animals in general. For example, heavy-tailed distributions of displacements have been observed in some bird species and associated with optimal search strategies (Boyer et al. 2009; Reynolds 2012; Viswanathan et al. 1996). However, alternative strategies may become more advantageous under certain conditions (Palyulin et al. 2014). While some examples focus on the cognitive abilities of foragers, other approaches emphasize the emerging patterns in the use of space resulting from interactions between animal behavior and the spatial structure of their environment. Regarding this issue, it is well established that animals do not use all available space but instead prefer to remain in a limited region known as their home range. Although home range assessments for the Chaco Tortoise (Chelonoidis chilensis) have not been reported, these tortoises are known to be range residents, typically using a subset of the available space within their environment (Kubisch and Echave, pers. comm.). That area supports their entire annual cycle of vital activities, including mating, nesting, and brumation.

Movement is a critical activity for most animals, as it allows them to search for food and water, evade predators, and migrate to environments more suitable for sustaining life and reproduction (Abramson et al. 2014; Blake et al. 2021; Kazimierski et al. 2015, 2016). For animals that play an important role as ecosystem engineers—thus affecting the distribution and abundance of other organisms through herbivory, disturbance, and seed dispersal—understanding their movement patterns is key to preserving their role in the community (Blake et al. 2012; Gibbs et al. 2010; Hamann 1993; Hunter et al. 2021). However, little is known about the movement patterns of many species, including the focus species of this study, C. chilensis. This gap in knowledge limits our ability to fully understand and protect their ecological contributions (Varela and Bucher 2002).

Chelonoidis chilensis inhabits the ecoregions of the dry Chaco, Monte plains and plateaus, the southern portion of the Espinal, and a few localities in the border zone between the dry and humid Chaco (Burkart et al. 1999; Sánchez et al. 2014). This species is distributed from southwestern Bolivia and western Paraguay to the northern part of the Province of Chubut in Argentina (Richard 1999). This species has the southernmost continental distribution of any tortoise in the world (Cei 1986). Chelonoidis chilensis is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and categorized as Endangered by the International Union for Conservation of Nature (Kubisch et al., in press). The main factors that have contributed to its decline include habitat reduction, modification, and destruction due to the expansion of the agricultural frontier, as well as the wildlife trade, since it is the most trafficked native reptile in the illegal pet market of Argentina (Prado et al. 2012). Furthermore, the threat to this species is being exacerbated by the introduction of exotic predators such as wild boar (Sus scrofa L., 1758; Kubisch et al. 2014).

Chelonoidis chilensis is an herbivorous species that feeds primarily on leaves and stems, as well as flowers and fruits from various plant families, including Gramineae, Malvaceae, Cactaceae, Solanaceae, Rhamnaceae, and others (Richard 1994). It is a potential seed disperser, as the germination capacity of some plant species has been observed to increase when they pass through this tortoise's digestive tract (Varela and Bucher 2002). However, little is known about how much or even how *C. chilensis* moves and, therefore, to what extent its movement may contribute to the distribution of vegetation across the landscape.

This species shows a pronounced sexual dimorphism in adulthood, with males being noticeably smaller than females, which is the opposite of the other species in this genus in which males can have three times the body mass of females (Kubisch et al. 2021). In the southernmost distribution of C. chilensis, the activity period is the shortest, due to a brumation (winter recess period) lasting around five months. Activity resumes at the beginning of spring (September in the southern hemisphere), with mating mostly observed between November and December (late spring). During the summer months from January to March, females spend significant time searching for suitable soil for nesting and laying eggs (pers. obs.). Despite these observations, much remains to be learned about the biology of C. chilensis populations in Argentina (Prado et al. 2012).

To rectify this lack of information, the objective of this study was to characterize the movement of *C. chilensis* in one of its southernmost populations during two key seasons within its period of activity. Specifically, we measured the maximum distance traveled in a single day, the daily home range, the velocity of movement, the mean square displacement, and the tortuosity of the

trajectories (related to the number and angles of turns), using three complementary tracking techniques. We hypothesized that during late spring (mating season), both males and females travel similar distances, as males continuously follow the females to copulate.

Understanding the movement patterns of this species is fundamental for comprehending its ecological role within the ecosystem and for designing effective management policies for this species and its habitat.

#### **Materials and Methods**

Study site. This study was conducted on a ranch located about 20 km north of the city of San Antonio Oeste, Province of Río Negro, Argentina. The site comprises a small section of the ranch, approximately 25 ha, which supports a stable population of *C. chilensis*. The area belongs to the Monte Austral phytogeographic unit, which is characterized by a shrub steppe with a predominance of *Larrea* spp. with multiple strata. The lower stratum consists of grasses and herbs, all with sparse coverage, and notably with very few cacti (Oyarzabal et al. 2018).

The specific study area is characterized predominantly by vegetation with xerophytic traits, consisting mainly of grass clumps (Poaceae) and shrubs. The most common shrubs species is *Larrea divaricata* (León et al. 1998; Morello et al. 2012). The region is arid, with sandy soils, scarce annual rainfall (~255 mm) concentrated in spring and fall, and significant daily temperature fluctuations (average 14.5 °C, extremes from –11.5 °C to 44.6 °C). Persistent winds from the west and southwest exacerbate the aridity (Godagnone and Bran 2008).

*Monitoring systems*. To study the movement trajectories of the tortoises, we employed a combination of monitoring techniques. First, we used the spool-and-line method,

which allows for precise and accurate description of trajectories. Second, we used radiotelemetry, where tortoises fitted with radio transmitters were located in the field using an antenna-receiver system. Finally, we employed a GPS-system developed in-house, which included inertial sensors and a temperature sensor in addition to the GPS unit.

Spool-and-line technique. The spool-and-line technique is widely used to obtain precise trajectories of various animals such as mammals (Cunha and Vieira 2002; Delciellos et al. 2019; Miles 1976), lizards and snakes (Law et al. 2016; Tozetti et al. 2009), and chelonians including tortoises (Breder 1927; Famelli et al. 2016). This method involves attaching a spool of thread to the back of the animal, with one end of the thread tied to a fixed point on the substrate. As the animal moves, the thread unwinds and locks onto the different substrates, allowing for reconstruction of the animal's trajectory. The spools used in our study measured 3.5 cm  $\times$  1.2 cm, contained 100 m of thread, and weighed approximately 2.5 g (Danfield Cotton Cocoon Bobbins; Fig. 1A). These spools are designed to unwind easily from the center, without requiring the spool itself to spin. By following the thread, we could accurately reconstruct the trajectory of each individual, providing detailed information on movement at small scales. This small-scale information is extremely important for this study, and potentially valuable for conservation research (Steinwald et al. 2006). For example, we used this technique to study the tortuosity of the tortoises' trajectories. It also serves as an efficient way to confirm the absence of nocturnal movement—if a spool placed on an individual at night remains unwound the following morning, it suggests there was no movement overnight.

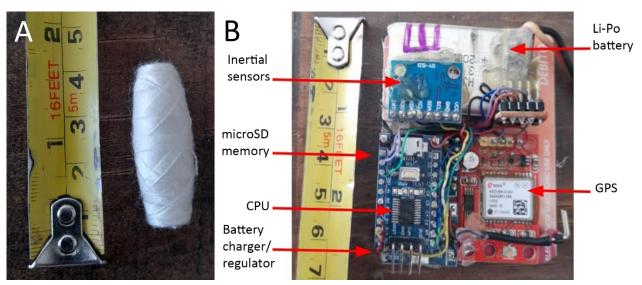


Fig. 1. (A) Spool used to monitor the movement of *C. chilensis*, with dimensions of 3.5 cm × 1.2 cm, 100 m of thread, and a weight of about 2.5 g (Danfield Cotton Cocoon Bobbins). A tape measure is included to show the scale. (B) Navigation unit for monitoring individuals, which consists of a GPS (UBlox NEO6), accelerometers, gyroscopes, and a temperature sensor (InveSense MPU6050) connected to a control and processing unit (ST Electronics STM8S103F3P6), and is powered by a battery charged through a regulator (134N3P), all weighing less than 45 g. The GPS position data, as well as data from inertial and temperature sensors, are saved in a 16 GB microSD memory card. A tape measure is included to show the scale.

A set of complementary techniques must be used to perform a comprehensive movement analysis, as the spool-and-line technique does not provide temporal information. Furthermore, its use is limited by the length of the thread and requires the researcher to manually retrace the path with a GPS device to record the different locations that were visited by the animal. By combining the precision of this technique with the methods described below, we could achieve a detailed characterization of the tortoises' trajectories.

Radiotelemetry technique. The radiotelemetry technique allows the tracking of individuals using a transmitter-receiver-antenna system (Gottwald et al. 2019; Kazimierski et al. 2021b; Mennill et al. 2012). We used Holohil transmitters (Grand HOLOHIL Systems Ltd. RI-2B) attached to each tortoise's carapace with tape. These transmitters emit pulses at a fixed frequency of around 150 MHz every 2 sec. These pulses were detected by a reception system consisting of a Yagi-Uda antenna connected to an ATS R410 receiver (Advanced Telemetry Systems, Inc.). This technique allowed us to accurately locate the transmitter and, with the help of a portable GPS device (Garmin eTrex x20), determine the exact positions of the tortoises.

Although this technique provides high spatial accuracy, it lacks the temporal resolution necessary to reconstruct reliable trajectories. In addition, this procedure may disturb the animal's behavior, as the researcher must approach the tortoise multiple times with the equipment (depending on the animal's velocity) in order to assess its position. This frequent proximity can interfere with natural behaviors, thereby affecting the monitoring results.

GPS-based system. The third technique used in this study offers high temporal resolution for tracking trajectories without disrupting animal behavior, thereby complementing the other two methodologies. We designed and developed low-cost navigation units to monitor individuals in their natural habitat. These units consist of a GPS receiver, inertial sensors (accelerometers and gyroscopes), and a temperature sensor (Fig. 1B). As a device developed by our research group, it met the necessary size and weight requirements of this study and offered configurable features, such as the GPS acquisition rate. The device is powered by a rechargeable battery, providing an autonomous period of approximately 15 h with a GPS acquisition rate of 5-10 min. Data from the GPS receiver and inertial sensors are stored on a micro-SD memory card on board. At the end of each monitoring day, we removed the micro-SD card for data download and the unit's batteries were recharged.

In this article we present data obtained with our first prototype, which was manufactured using off-theshelf electronic modules. The components are listed in the caption of Fig. 1. The hardware was designed to be cost-effective and easy to construct, with modules connected using the wire-wrap technique. The firmware was optimized to extend the device's autonomy and is freely available in an open repository (Kazimierski et al. 2021a).

Despite the superior performance of the GPS units compared to the radiotelemetry technique, we only had eight units available for use during each field season. As a result, they were complemented with radiotelemetry to monitor a larger number of individuals. Furthermore, the position errors associated with radiotelemetry are smaller than with the GPS-based method, so the use of both techniques in parallel allowed us to compare and optimize the results.

Field work. Data were collected during two field seasons of C. chilensis in the natural habitat. Specifically, we monitored the tortoises from 29 November to 3 December 2020 (spring season) and from 10–15 January 2021 (summer season). During the 2020 field season, we used the spool-and-line technique to track seven individuals, radiotelemetry to monitor 12 individuals, and the GPS system for six individuals. During the 2021 campaign, we monitored four individuals using the GPSbased system. Monitoring sessions began around 0700 h and ended around 2100 h local time (UT-3). The tortoises monitored were those visually located in the field. Upon finding an individual, the monitoring device was attached using adhesive tape (<sup>©</sup>Duck Tape, Real Tree Hardwood Camouflage; Fig. 2) and the animal was released at the location where it was initially found.



**Fig. 2.** Male individual of *Chelonoidis chilensis* monitored with the navigation device on the top of its shell, attached with camouflage tape.

The weight of the device including the battery and GNSS receiver was 44.9 g (Kazimierski et al. 2023) and the lightest tortoise weighed around 1 kg, so the device represented ~4.5% of its body weight, which is consistent with tracking guidelines. Camouflage tape was used to mimic the environment, and no sharp corners were left exposed to prevent the tortoises from becoming

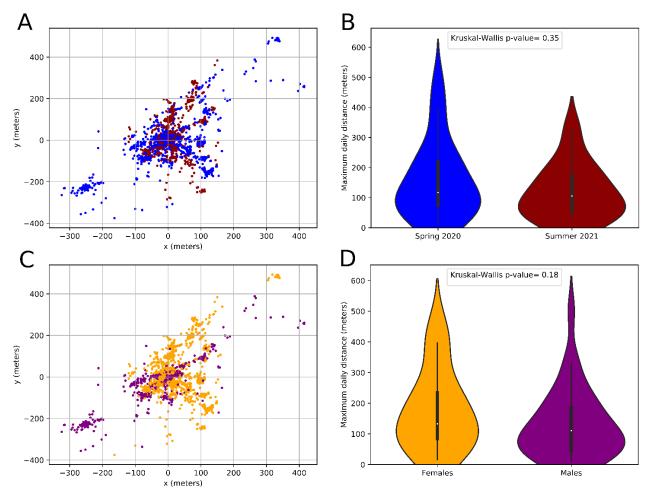


Fig. 3. (A) Estimated positions of the tortoises, relative to a common origin, using the radiotelemetry and GPS-based systems during spring 2020 (blue) and summer 2021 (red). For each tortoise, the position at the beginning of the day was shifted to the point (0,0) and the axes are scaled in meters. (B) Distribution of the data for maximum distance from the starting point for each tortoise and for each day during spring 2020 (blue) and summer 2021 (red). (C) Estimated positions of the tortoises relative to a common origin using the radiotelemetry and GPS-based systems for females (yellow) and males (violet). Each tortoise's position at the beginning of the day was shifted to the point (0,0) and the axes are scaled in meters. (D) Distribution of the data for maximum distance from the starting point for each tortoise and for each day for females (yellow) and males (violet).

entangled in the branches. All work was conducted under the appropriate permits (Resolution 034-2020) issued by the Secretariat of Environment and Sustainable Development and Climate Change of Río Negro. The animals were handled as little as possible, following the approved protocol of the Institutional Committee for the Care and Use of Laboratory Animals or Experimentation (CICUAL; N° 2020-015) of INIBIOMA. This protocol includes measures to reduce stress, hyperthermia, fluid loss, and the transmission of diseases, to ensure the animals' safety throughout the study.

Data analysis. To assess the maximum area covered by the tortoises monitored using radiotelemetry and GPS-based techniques, we calculated the convex hull for each daily tortoise trajectory. In this context, these "hulls" are the smallest convex polygons enclosing all the points of a given daily trajectory and were determined using the ConvexHull function from the scipy.spatial module (Virtanen et al. 2020).

In addition to the trajectory descriptions, GPS data allowed us to estimate the tortoises' velocity and the mean square displacement (MSD). These data give a measure of the dispersal of self-propelled agents, providing insight into their spatial movement patterns and, specifically, how these patterns differ from purely diffusive behavior.

Given that the set of maximum distances represents a small subset of all trajectory points and is presumably not normally distributed, we used the non-parametric Kruskal-Wallis test to assess whether the distributions of daily dispersion differed by season or sex.

Radiotelemetry and GPS-based techniques are imprecise for characterizing the distribution of turning angles, which highlights the importance of using a combination of methods. Trajectories tracked using the spool-and-line technique offer much finer spatial resolution compared to both radiotelemetry and GPS, so we studied the distribution of turning angles using the spool-and-line trajectories.

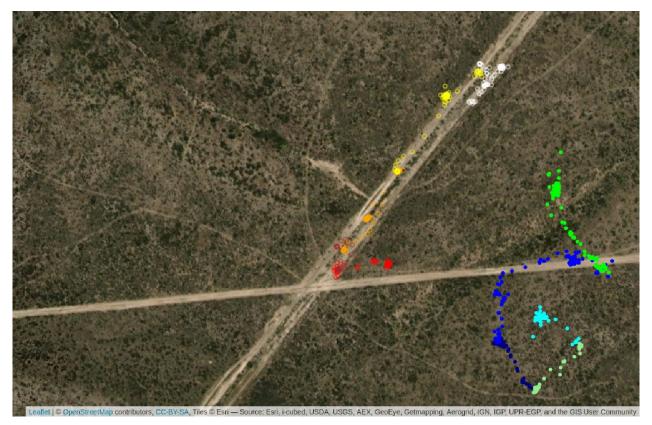


Fig. 4. Measured trajectories using the GPS-based system, where each color represents a consecutive monitoring day. The left trajectory, marked with open circles, corresponds to a male individual during summer 2021 (from 10 January 2021, in red to 14 January 2021, in white). The right trajectory, marked with filled circles, corresponds to a female individual during spring 2020 (from 29 November 2020, in light blue to 3 December 2020, in light green).

Both radiotelemetry and GPS-based techniques have significant errors in accurately characterizing the tortuosity of the tortoises' paths. For the radiotelemetry system, the error was estimated by recording 10 consecutive position measurements using the same equipment within a one-minute interval at the study site. The error for the GPS-based system was estimated by monitoring an individual tortoise's position over 400 min (recording one position every 10 min) during the night. To ensure that the animal remained stationary, we simultaneously tracked it with the spool-and-line technique, confirming that no movement had occurred during that period.

# Results

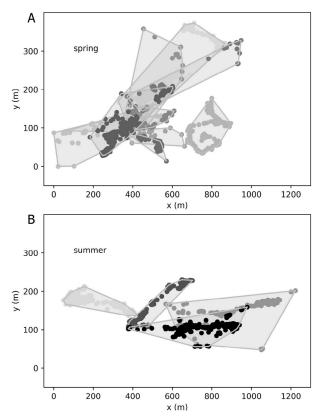
For the trajectories obtained for each tortoise using the radiotelemetry and GPS-based techniques, we show the data separated by season (Fig. 3A-B) and according to sex (Fig. 3C-D). This graphical representation provides a clear visualization of the movement and the distances covered by a tortoise over the course of a day.

Figure 4 shows two examples of trajectories obtained with the GPS-based system corresponding to two different individuals and seasons, a female monitored during spring and a male tracked during summer.

To characterize these trajectories, the maximum distance from the starting point was calculated for each day and each tortoise, distinguishing between seasons (Fig. 3B) and sexes (Fig. 3D). The Kruskal-Wallis test showed that the distributions were statistically indistinguishable by season (H = 0.862, p = 0.353) and by sex (H = 1.817, p = 0.177).

The mean maximum distance covered was about 110 m for both sexes and seasons. However, the distances showed significant variability, with maximum distances ranging over 400 m (Fig. 3). We then calculated the convex hull for each daily tortoise trajectory (Fig. 5). The average maximum area covered by each tortoise on a daily scale was estimated to be  $864 \pm 283$  m² during the spring season and  $1,034 \pm 298$  m² during the summer season.

The distribution of the tortoise velocity is primarily unimodal, with a mode of  $0.4 \pm 0.1$  m/min and a median of  $0.6 \pm 0.1$  m/min (Fig. 6A). For the MSD, the tortoise movements in this study were subdiffusive (Fig. 6B), suggesting that the balance between dispersing in the exploration of new areas and perusing their home ranges leaned toward the latter. In other words, the time taken to travel from one point to another was shorter than the time spent by a random walker, at least on a daily scale. Very long steps (on the order of the daily home range)



**Fig. 5.** Convex hulls for the trajectories assessed by GPS-based and radiotelemetry monitoring during spring season 2020 (upper panel) and summer season 2021 (lower panel). The shadowed areas constitute the maximum area covered by each tortoise in the corresponding season.

were uncommon, supporting the notion that tortoises primarily moved within a daily home range. Although the spatial region of activity may vary from day to day, their movement on a daily basis was slower than that of typical diffusion.

The mean positional error of the radiotelemetry technique was found to be 0.45 m, with a standard deviation of 0.54 m and a maximum recorded error of 1.4 m. The mean value of the distribution of positions recorded with the GPS system during the night was 3.15 m, with a standard deviation of 3.17 m and a maximum value of 11.25 m.

The distribution of turning angles obtained from spool-and-line trajectories during the 2020 and 2021 field seasons (Fig. 6A, inset) reveals that most angles show minimal deviation from a straight line. This pattern suggests that tortoises often move with a clear directional focus, rather than making random or frequent turns.

# **Conclusions and Discussion**

In this study, the trajectories, velocity, home range, and mean square displacement of 29 tortoises were investigated using three techniques to compare the movement patterns among seasons and sexes, and support the management of Chaco Tortoises. The spooland-line, radiotelemetry, and a GPS-based system were

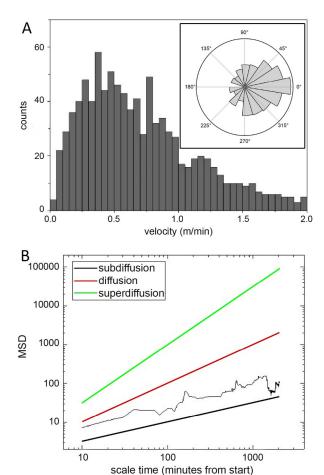


Fig. 6. Characterizations of the trajectories. (A) Distribution of tortoise velocities. The mode of the distribution is  $0.4\pm0.1$  m/min and the median is  $0.8\pm0.1$  m/min. This distribution is derived from the analysis of data from the GPS-based system placed on six individuals (2020) and four individuals (2021). Inset: Distribution of 340 turning angles measured with spool-and-line technique during 2020 and 2021. The radius of the circle corresponds to around 25% of the turning angles. (B) MSD of monitored tortoises (thin black line), estimated using the 2020 and 2021 data recorded with the GPS-based system. The solid black line is shown to guide the eyes and corresponds to subdiffusive movements, while the red and green lines are shown for comparison and correspond to diffusive and superdiffusive movements, respectively.

employed to monitor the movement patterns of *C. chilensis* in their natural habitat. Each method provided distinct advantages, allowing us to generate an initial comprehensive dataset on tortoise movement, while also addressing the limitations in spatial or temporal resolution through methodological complementarity.

The spool-and-line technique was particularly valuable for generating precise trajectories, which is essential for quantifying the tortuosity of the walks. This aspect is crucial, because accurately assessing tortuosity requires high-resolution data, which GPS systems might underestimate when sampling intervals are too sparse. We found that spool-and-line data are ideal for such analyses, and the data suggested a potential correlation between movement twists and the substrate at the scale of individual plants. We plan to explore this topic further

with ongoing vegetation surveys.

For broader monitoring, the radiotelemetry and GPS-based methods allowed us to track more than 10 individuals during spring 2020 and summer 2021. We were able to study both the temporal evolution and the spatial properties of their movements using this approach. Our data indicate that the average maximum daily distance covered by tortoises was approximately 110 m, with some individuals traveling up to 400 meters. These findings are compatible with those reported for the (ecologically similar) Mojave Desert Tortoise Gopherus agassizii (Cooper 1863; Franks et al. 2011). Such dispersion in the traveled distance might be caused by environmental factors, such as drought periods (Duda 1999), rainfall, or temperature (Falcon et al. 2018). Movement patterns in both species may be strongly influenced by environmental factors, highlighting their behavioral plasticity in coping with arid conditions. We will explore these relationships further in future studies. Similarly, radiotelemetry studies on Mojave Desert Tortoises have reported daily movement distances within a comparable range, further supporting the influence of environmental conditions on movement patterns (Franks et al. 2011).

Our findings are also similar to those for Galapagos Giant Tortoises, which are phylogenetically the closest relatives of *C. chilensis*. Their daily movements follow basically circular routes, often beginning and ending at a site where they slept, with a daily travel distance between 21 and 413 m (Blake et al. 2021). However, some species from the large Galapagos Islands also undertake long-distance seasonal migrations (Blake et al. 2013).

The distances that tortoises travel per day can vary according to sex, size, and time of year (Aguirre et al. 1984; Eubanks et al. 2003; Guyer et al. 2012). For example, females of *Gopherus flavomarginatus* (Legler, 1959) showed a negative correlation between carapace length and the average distance moved per day. On the contrary, the juveniles showed a positive correlation, but males did not show any relationship between carapace length and the distance moved per day (Aguirre et al. 1984). In this study, the mean travel distance did not show a difference between males and females, despite the marked difference in size.

Regarding the used area, C. chilensis remained within a DHR of  $864 \pm 283$  m² (spring season) or  $1,034 \pm 298$  m² (summer season). We found no difference in the area covered by the trajectories during the mating season (spring) and the summer season. In addition, the daily area covered by males during the spring season was similar to that covered by females, supporting the observation that male and female trajectories greatly overlap during this period, as males persistently followed the females. In  $Gopherus\ polyphemus$  tortoises (Daudin, 1802), females move more frequently in the summer months and males exhibit a peak in movement prior to mating activity (Eubanks et al. 2003), traveling longer distances than

the females (Guyer et al. 2012). However, testing these hypotheses will require a larger number of monitored individuals to explore any significant differences in daily displacements and area visited according to sex and season.

The data in this study revealed interesting patterns regarding the spatial use of the terrain. Notably, the tortoises frequently used internal paths within the study area (e.g., the left trajectory in Fig. 4). This behavior of using open areas for movement has also been observed in Galapagos Tortoises that make use of cattle trails, although it was unclear whether those trails were made by the tortoises and then used by the domestic animals or vice versa (Blake et al. 2021). In addition, tortoises were more frequently found near ponds and along low-traffic roads (Pike et al. 2023). Understanding how these routes are selected could provide insights into habitat preference and territorial behavior.

Chelonoidis chilensis typically moved with a most probable velocity of  $0.4 \pm 0.1$  m/min, with a median of 0.8 $\pm$  0.1 m/min. The velocity distribution can be improved by acquiring data with higher temporal (e.g., increasing the GPS sampling rate) and spatial (e.g., quantitatively incorporating the information from inertial sensors) resolution. The current data suggest the possibility of additional modes in the velocity distribution at around 0.8 and 1.2 m/min. For instance, the higher velocity modes could be characteristic of searching behavior, while the slower ones could be indicative of an ambling mode. At this stage, these modes cannot be definitively confirmed; and complementing the quantitative results with behavioral observations in the field would be useful to investigate this topic further. In fact, during early spring, we observed that males seem to spend a considerable part of the day walking around in search of mates.

The spatial and temporal resolution of the GPS data allowed us to characterize the MSD, in addition to determining the speed of movement. The MSD is a measure of the evolution of movement as a function of time. For example, random movement typically results in an MSD that grows linearly with time. Cases where the MSD grows sublinearly or superlinearly over time are referred to as "subdiffusive" or "superdiffusive," respectively. The mean squared displacements observed in the tortoises showed sublinear growth (Fig. 6, black thin curve), meaning that the tortoises took more time than a random walker to move from one place to another. This result could be due to multiple factors, such as the existence of multiple waiting points throughout the tortoise's trajectory, or the heterogeneity of the substrate on which the individual walks (Bouchaud and Georges 1990). In the context of random walks, subdiffusive behavior is usually associated with waiting time distributions between steps that have fat tails (Klages et al. 2008; Kumar et al. 2010; Metzler and Klafter 2000, 2004). However, subdiffusive regimes can be also associated with correlated random walks, such as those influenced by memory effects (Bouchaud and Georges 1990). Additional behavioral observations will be important for better understanding of the origin of this significant result.

Understanding the patterns of movement and habitat use is crucial for developing effective conservation, restoration, and management strategies for this species of tortoise. Without a thorough assessment of their basic biology, we cannot determine the extent to which they are affected by habitat fragmentation. In the Monte Austral, near San Antonio Oeste, the main economic activity is extensive cattle ranching. This practice began spreading in the last 30 years, so it is relatively recent given the tortoises' long life cycle. Cattle are known to produce profound and often irreversible changes in both the vegetation and soil across large areas of Patagonia (Borrelli and Oliva 2001; Paruelo et al. 1993). For example, soil compaction by livestock can destroy tortoise shelters and prevent young tortoises from emerging from trampled nests (Waller and Micucci 1997). The study site itself is an unmanaged field that maintains a pristine ecosystem. However, facilities are currently being prepared to introduce cattle into the area. The impacts of these changes in ground conditions and vegetation on the movement of this endangered tortoise remain uncertain.

Similarly, it is important to evaluate the ecological role of tortoises as seed dispersers for key shrub species in the Monte Austral biome. The dynamics of plant populations depend heavily on pollination and seed dispersal, both of which are closely linked to the movement dynamics of the disperser animals (Morales and Carlo 2006). In recent years, there has been a surge in studies examining the roles of reptiles in pollination and seed dispersal (Galindo-Uribe and Hoyos-Hoyos 2007). For example, lizards and tortoises have recently been shown to be the most important seed dispersers in some areas of the Galapagos Islands (Galindo-Uribe and Hoyos-Hoyos 2007; Nogales et al. 2017) and were more efficient than birds in the dispersal of some plant species in a community of the Canary Islands (González-Castro et al. 2015). Understanding their interactions with plant species is vital, particularly in areas undergoing habitat change.

A related issue is the consumption of fruits by tortoises, which could affect the reproduction of several species of plants and impact the structure of vegetation within a community (Jerozolimski et al. 2009; Richardson and Stiling 2019; Stevenson and Guzmán 2008). These studies highlight not only the ecological importance of tortoises but also their potential economic role in promoting the reproduction and dispersal of economically important plants (Valencia-Aguilar et al. 2013). Tortoises serve essential roles in ecosystems as prey, foragers, and especially as seed dispersers (Blake et al. 2012; Hamann 1993). However, substantial work remains in collecting and analyzing data, as well as improving methodologies,

to deepen our understanding of this endangered species. From the movement trajectories, it may be possible to infer a probability map of locations for seed dispersal, which could enable the modeling of an expected vegetation distribution and, ultimately, quantifying the role of tortoises as ecosystem engineers.

In conclusion, while significant progress has been made in understanding the movement ecology of *C. chilensis*, many key aspects remain to be explored. Increasing the sample size of monitored individuals, refining the methodologies, and expanding field observations will help to build a more detailed picture of how these tortoises navigate their environment. Such insights are essential not only for the conservation of *C. chilensis* but also for understanding their role in the broader ecosystem. Addressing these questions is critical as we work toward the preservation and sustainable management of their habitats in the face of anthropogenic pressures.

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# Movement of the Chaco Tortoise

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#### Kazimierski et al.



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