Unraveling key aspects of the vulnerable Chelonoidis chilensis tortoise in the wild

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ABSTRACT

Chelonoidis chilensis is the southernmost species of tortoise in the globe and is in a vulnerable state because of the reduction of its habitat and due to its value in the illegal pet market. Despite its relevance, there is a lack of knowledge regarding the behaviour of *C. chilensis* in the wild and many basic questions about its biology remain unanswered, particularly about their movement. Based on observations and previous studies, we predicted that tortoises move in a bounded region of space, returning to recurring refuges and moving in a limited area of use. To verify this prediction, we monitored the movement of individuals of this species using different and complementary techniques: spool-and-line, radiotelemetry and GPS-based (developed by our team). We implemented these techniques during two campaigns, in which we monitored 12 individuals with radiotelemetry, 10 using the GPS-based system and 7 with the spool-and-line technique in their natural habitat near San Antonio Oeste, RíoNegro, Argentina. We analyzed the mean square displacement of the obtained trajectories, indicating a subdiffusive type of movement, which is consistent with the idea that they move in a bounded region of space. We also hypothesized that the movement and that bounded region of space in which they move depends on the season of the year; specifically, that the individuals travel greater distances during the mating season (spring) than during the egg deposition season (summer). After the analysis of the trajectories obtained, we found greater displacements in the spring than in the summer. Additionally, we found that this individuals are capable of traveling up to 400 meters a day; we also measured the tortuosity of their trajectories and the velocity of movement, with 0.4 ± 0.1 m/min being the most probable value.

The findings that we report in this work answer basic questions about the movement and behavior of this species in their natural habitat, which will have a significant impact on the establishment of guidelines that contribute to their conservation.

Keywords: GPS positioning; Habitat use; Inertial sensors; Radiotelemetry technique; Spool-and-line technique

INTRODUCTION

The study of movement and behaviour of small animals is important for understanding their ecological roles, their response to environmental changes, and their conservation status. Reptiles, as ectothermic organisms, are highly sensitive to changes in temperature, precipitation, and habitat structure, which can affect their survival, reproduction and dispersal (Boretto et al., 2014; Ibargüengoytía et al., 2020; Kubisch et al., 2016, 2023). In the case of endangered species, tracking their movement and behaviour is critical for answering basic questions about their biology, and for developing effective conservation strategies and mitigating the threats to their populations. In this context, the task poses significant challenges, such as the size of the animals, the complexity of their habitats, and the availability of the technology for tracking and monitoring them. To address these challenges, recent advances in technology and methodology have been applied to tracking small reptiles and other animals. For instance, radio telemetry, GPS tracking, and accelerometry have been used to collect data about the habitat use, home range, activity patterns, and thermal preferences of reptiles in different ecosystems (Lagarde et al., 2008; Guzmán et al., 2008; Famelli et al.; 2016; Liuzzo et al., 2023). These methods have also enabled researchers to test hypotheses about the ecological factors that affect reptile behaviour (Arfuso et al., 2022), such as the effects of habitat fragmentation, climate change, and human disturbance. Additionally, the integration of remote sensing, modeling, and network analysis has provided a comprehensive understanding of the spatial and temporal dynamics of reptile populations and their interactions with other species and ecosystem processes.

Animal movement patterns generally depend on the environment, intrinsic factors of individuals and interactions with others (Morales et al., 2005, 2010; Nathan, 2008; Smouse et al., 2010). The complexity of these movements is manifested in their trajectories. In the case of foragers, these depend strongly on the vegetation, which preeminently determines the movement. The dynamics of the plant community is, in turn, dependent on foraging, pollination and seed dispersal (Morales and Carlo, 2006), in a mutualistic interaction of primary importance in many ecosystems. In particular, tortoises have an important role as ecosystem engineers, manipulating the distribution and abundance of other organisms through the direct effects of herbivory, disturbance, and seed dispersal with consequent indirect impacts on animal communities (Hamann, 1993; Gibbs et al., 2010; Blake et al., 2012; Hunter et al., 2021; Macdonald et al., 1988; Guzmán et al., 2008). In such a context, which are the trategies that an animal adopts for optimal foraging? Which ones are possible under different hypotheses of animal perception and memory? (Krochmal et al. 2023; Bartumeus et al., 2002; Barton et al., 2009; Fronhofer et al., 2013). There is still much discussion regarding search paths and whether the so called Lévy walks or Lévy flights are predominant in nature or not (Viswanathan et al., 1996; Reynolds, 2012; Boyer et al., 2009). While some focus on the cognitive abilities of foragers (Krochmal et al. 2023), other approaches consider the study of emerging patterns in the use of space as a result of the interactions between the behaviour of animals and the spatial structure of the environment and the resource availability (Blake et al., 2021; Abramson et al., 2014; Kazimierski et al., 2015, 2016). For many species, a lack of knowledge of their behaviour in the wild still precludes addressing these matters. The characterization of the trajectories is the first important study to undertake.

In many countries, access to commercial monitoring devices is often too expensive or difficult to obtain. Our interdisciplinary team has been designing and developing such devices for our own work in the field of animal behaviour for several years (Kazimierski et al. 2021). Furthermore, we aimed at producing a versatile system, suitable to be adapted to particular needs of species and habitats through simple software or hardware modifications (Kazimierski et al. 2023). In the present work, we demonstrate the capabilities of our system applied to the movement of one of our species of interest, the Chaco tortoise, *Chelonoidis chilensis* (Gray, 1870).

The tortoise *C. chilensis* is the tortoise with the southernmost continental distribution in the world (Cei, 1986). Inhabits several ecoregions of South America: the dry Chaco, Monte plains and plateaus, the southern portion of the Espinal, and a few localities in the border zone between the dry Chaco and the humid Chaco (Sánchez et al., 2014; Burkart et al., 1999). It is distributed from the southwest of Bolivia and the west of Paraguay to the north of the province of Chubut, in Argentina (Richard, 1999). This species is included in Appendix II of the *Convention on International Trade in Endangered Species of Wild Fauna and Flora* (CITES) and it has been categorized as “vulnerable” at the national (Prado et al., 2012) and international levels by the International Union for Conservation of Nature (IUCN 2014[1]). The main factors that led to this situation are the reduction, modification and destruction of their habitat, due to the expansion of the agricultural frontier, and the wildlife trade, being the most trafficked native reptile in the illegal pet market of Argentina (Prado et al., 2012). Also, the threat to this species is exacerbated by the

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[1] Accessible at https://www.iucnredlist.org/species/9007/12949680.

recent introduction of exotic predatory species such as wild boar (*Sus scrofa* L., 1758; Kubisch et al., 2014). There is still much to learn about the biology of the *C. chilensis* populations present in Argentina (Prado et al., 2012; Cabrera, 2022; Gatica et al., 2021).

The diet of *C. chilensis* is herbivorous, they feed mainly on leaves and stems, as well as flowers and fruits of various species of the Gramineae, Malvaceae, Cactaceae, Solanaceae and Rhamnaceae families, among others (Richard, 1994). They are potential seed dispersers since it was observed that the germination capacity of some plant species increases when they go through their digestive tract (Varela and Bucher, 2002). However, it is not known how much or even how *C. chilensis* moves and, therefore, in what way their movement could contribute to the distribution of the vegetation in the landscape. In this study, we hypothesized that the individuals of *C. chilensis* have an area of use associated with their movement and this area varies with the time of year. In this sense, their area of use and the distances they travel affect the spatial distribution of the vegetation.

Lastly, regarding the difference between the sexes, this species shows a marked sexual dimorphism when they are adults. Males are noticeably smaller than females, contrary to what happens in the rest of the species of the genus, in which case males can even triplicate the size of the female (Kubisch and Ibargüengoytía, 2021). The activity period in *C. chilensis* southernmost distribution is the shortest of the species, because they experience a brumation for around five months. The activity period starts at the beginning of spring (September in the southern hemisphere) and, from November to December (still spring), it is when mating is mostly observed. Between January and March (summer in the southern hemisphere) females spend a significant amount of time searching for suitable soil for nesting and to lay eggs (personal observation). We consider that, since both males and females move in search of a mate in the mating season (spring) there will be greater displacements and distances traveled, as well as a greater area associated with movement than in the season when it is only the females that move to look for nests (summer).

MATERIALS AND METHODS

This work includes field work, monitoring of *C. chilensis* individuals in their natural habitat, and data analysis. We separate this section into subsections to detail how the fieldwork and monitoring was carried out.

Study site

The study was carried out in a ranch located about 20 km north of San Antonio Oeste city, Río Negro, Argentina. The site consists of a small area of the ranch, approximately 25 hectares where there is a stable population of *C. chilensis* with a large number of specimens. The area belongs to the Monte Austral phytogeographic unit, characterized by a shrub steppe with a predominance of *Larrea spp*. with several strata, the lower one being grasses and herbs, all with very little coverage, and particularly with very few cacti (Oyarzabal et al., 2018).

The specific study area is characterized by a vegetation cover, mostly with xerophytic characteristics, with a predominance of grass clumps (Poaceae) and shrubs (the most frequent are *Larrea divaricata* Cav., *L. cuneifolia* Cav., *Lycium* L., *Chuquiraga* Juss., *Prosopis* L., *Ephedra* L., *Gutierrezia* Lag., *Verbena* L., and *Baccharis* L. (León et al., 1998; Morello et al., 2012). We can also find *Monttea aphylla* (Miers) Benth. and Hook.f., and isolated individuals or even small groups of *Geoffroea decorticans* (Hook. and Arn.) Burkart. Some other typical species of this area have also become very abundant, such as *Capparis atamisquea* Kuntze, *Chuquiraga erinacea* D.Don and *Condalia microphylla* Cav. (Bóo et al., 1997; León et al., 1998; Morello et al., 2012). In turn, the grass stratum has a higher species richness than the other Zygophyllaceae of the Monte steppes. The soil is rather sandy with a low percentage of clay and abundant pebbles. Limiting a sector of the study area, there is the *Gran Bajo del Gualicho*, a Patagonian plain of up to 70 meters below sea level, characterized by a high saline concentration. This is why there are more saline sectors, where we can find halophyte species such as *Suaeda divaricata* Moq. and several species of the genus *Atriplex spp* L. Scarce precipitations give an average of approximately 255 mm in the year, with minor peaks in spring and fall. Besides, an annual average temperature of 14.5 °C with significant daily thermal amplitudes and a persistence of the west and southwest winds, deepen the marked aridity of the region (Godagnone and Bran, 2008). The minimum average temperature is 1 °C, and the maximum is 30 °C, but nevertheless there are extreme recorded temperatures of –11.5 and 44.6 °C (data for 1961–2021 provided by the National Meteorological Service).

Monitoring systems

We have combined three monitoring techniques to study the trajectories of the tortoises to answer our questions about their movement and area of use. One of the techniques was the spool-and-line technique which allows a precise and accurate description of trajectories. The second one was a radio-telemetry technique to locate the tortoises by receiving, through an antenna-receiver system, the signal from a transmitter placed on them. Finally, the third technique consisted of an in-house developed GPS-based system, which contains inertial sensors and a temperature sensor in addition to a GPS. It is an evolution of the system we developed in Kazimierski (2021), and a first of the system describe in more detail in Kazimierski (2023). In the following subsections we provide details of each methodology.

Spool-and-line technique

The spool-and- line technique is widely used to obtain very precise trajectories of the animals. It is used for mammals (Miles, 1976; Cunha and Vieira, 2002; Delciellos et al., 2019), for chelonians (Breder, 1927), for lizards and snakes (Law et al., 2016; Tozetti et al., 2009) and, also, for tortoises (Famelli et al., 2016). This technique consists in attaching a spool of thread on the back of the individuals and tie one end of the thread to a fixed point on the substrate so that, as the animals move, the thread unwinds and locks onto the different substrates through which they pass. The dimensions of the used spools are 3.5 cm × 1.2 cm, containing 100 m of thread and weighing about 2.5 g (Danfield Cotton Cocoon Bobbins; Fig. 1A). These spools are assembled in such a way that the thread unwinds easily from the center and does not require the spool to spin. By tracking the thread, we can reconstruct the trajectory of each individual. This technique provides detailed information of movement at small scales, which is extremely important for this particular study, and could have a relevant application in conservation-related studies (Steinwald et al., 2006). In particular, we have used this technique to study the tortuosity of trajectories. In addition, it is an efficient way to register the lack of night movement; if we place the spool on an individual at night and it continues without unwinding the next day, we can infer that there was no movement during the night.

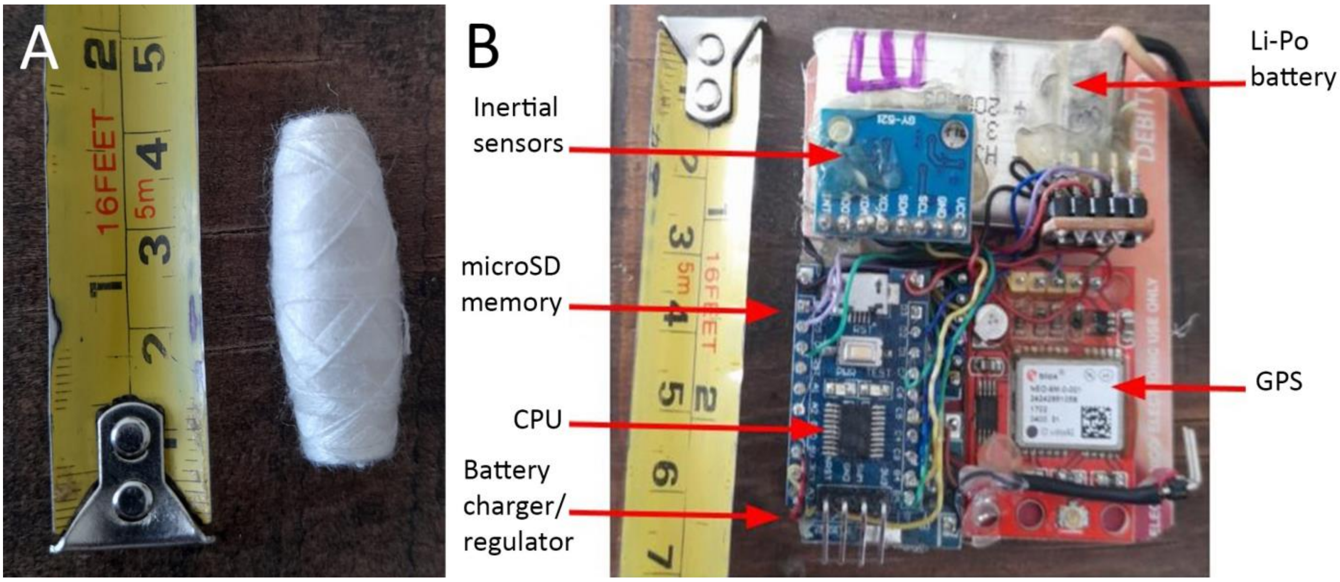

Figure 1. *A) Spool used to monitor the movement of C. chilensis. The dimensions are 3.5 cm × 1.2 cm, containing 100m of thread and weighing about 2.5 g (Danfield Cotton Cocoon Bobbins). A tape measure is shown to reference dimensions. B) Navigation unit to monitor individuals. It consists of GPS (UBlox NEO6), accelerometers, gyroscopes, and a temperature sensor (InveSense MPU6050) connected to a control and processing unit (ST Electronics STM8S103F3P6), and 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. A tape measure is shown as a reference dimension.*

A set of complementary techniques are necessary to perform a full movement analysis, since the spool-and-line technique does not provide temporal information. Furthermore, the study is restricted to the length of the thread, and requires the researcher to retrace the path with GPS, recording different visited sites. By combining the precision of this technique with those explained below, it is possible to have a detailed characterization of the trajectories.

Radiotelemetry

The radiotelemetry technique allows individuals to be located using a transmitter-receiver-antenna system (Mennill et al., 2012; Gottwald et al., 2019; Kazimierski et al. 2023). It is a technique that allows us to answer how far *C. chilensis* individuals are able to travel, to identify if they move inside a bounded region of space and to establish differences between seasons of the year. We employed Holohil transmitters (Grand HOLOHIL Systems Ltd. RI-2B) attached to tortoises' carapace using tape. These transmitters emit a pulse on a fixed frequency around 150 MHz every 2 seconds. These pulses are detected by a reception system that consist of a Yagi-Uda antenna connected to an ATS R410 receiver (Advanced Telemetry Systems, Inc.). This technique allows us to locate the transmitter with a great precision and, using a portable GPS (Garmin eTrex x20), determine the location.

Despite being spatially precise, this technique does not have the temporal resolution necessary to reconstruct reliable trajectories. Also, this procedure might disturb the animal behaviour, since the researcher should approach the animal several times with the equipment (depending on the animal velocity), in order to assess its position, therefore failing at monitoring the animal trajectory in natural conditions. In the following section we describe our third technique, that offers high temporal resolution of the trajectories without disturbing animal behaviour, complementing both previously described methodologies.

GPS-based system

We have designed and developed low-cost navigation units to monitor individuals in their natural habitat, which consist of a GPS receiver, inertial sensors (accelerometers and gyroscopes) and a temperature sensor (Fig. 1B). From the GPS data it is possible to survey the trajectories of the individuals and complement them with the data obtained using radiotelemetry to answer the questions of this work. Being a device developed by our research group, it meets the necessary size and weight specifications and has configurable features like GPS acquisition rate. The monitoring device was powered by a rechargeable battery that gave an autonomy of approximately 15 hours considering a GPS acquisition rate of 5–10 minutes. Data from the GPS receiver and the inertial sensors was stored in a micro-SD memory on board. At the end of each monitoring day, we removed and downloaded the micro-SD memory and recharged the batteries. In this work we present data obtained with our first prototype, manufactured with off-the-shelf electronic modules. The employed components are listed in the caption of Fig. 1. Its hardware was designed for a low cost and easy construction. Modules are connected using wire-wrap technique. Its firmware was designed to extend its autonomy and is freely available in the open repository (Kazimierski et al., 2021).

Despite its better performance compared to the radiotelemetry technique, we had eight of these units to use during these campaigns, so it was necessary to complement them with radiotelemetry technique in order to monitor more individuals. In addition, the error of the positions monitored with radiotelemetry is less than that of GPS-based methodology, thus it is worth using both to compare and optimize the results.

Field work

We analyzed the results of two campaigns monitoring the movement of *C. chilensis* in the natural habitat. Specifically, we monitored them from November 29th to December 3rd, 2020 (spring season) and from January 10th –15th, 2021 (summer season). During the 2020 campaign we used the spool-and-line technique to monitor seven individuals, radiotelemetry to monitor twelve individuals and the GPS system to monitor six individuals. During 2021, we monitored four individuals using the GPS based system. Monitoring began around 07:00 h and ended around 21:00 h local time (UT-3). The tortoises monitored were those found visually in the field. Upon finding them, the device was placed using adhesive tape (©Duck Tape, Real Tree Hardwood Camouflage; Fig. 2) and the animal was released at the same place where it was found.

Figure 2. *Male individual of Chelonoidis chilensis monitored with the device on top of his shell attached with camouflage tape.*

The weight of the equipment did not exceed 10% of the body mass of the animals and did not disturb their daily activity. A camouflage tape was used to mimic the environment and no sharp corners were left to prevent the tortoise from getting trapped between branches. We have worked with the pertinent permits (Resolution 034-2020) granted 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 by the Institutional Committee for the Care and Use of Laboratory Animals or Experimentation (CICUAL; N° 2020-015) of INIBIOMA, which includes techniques to reduce stress, hyperthermia, fluid loss and the transmission of diseases, in order to guarantee their safety.

Analysis of data

The data analysis of the obtained trajectories was performed using the programming language Python. To allows easily visualize how far a tortoise moves during one day, we graficated the estimated positions of the tortoises, relative to a common origin, separated data between seasons (spring and summer). We also studied the Mean Square Displacement (MSD), a measure to quantify the average displacement of the animals over time in their trajectories. The MSD provides insight into the type of motion exhibited by them. If the MSD increases linearly with time it indicates normal diffusion and, if the MSD increases sub-linearly with time, it may suggest confined motion. For the assessment of the maximum area covered by the tortoises monitored using radiotelemetry and GPS-based techniques, we computed the convex hull of each tortoise trajectory. These hulls are, in our case, the smallest convex polygons enclosing all the points of a given trajectory and were determined using the Python function ConvexHull of the library *scipy.spatial*.

For the analysis of the trajectories it was necessary to know the error of each technique. The radiotelemetry and GPS-based techniques have a considerable error when it comes to characterizing the tortuosity of the paths, as will be explained in the following. The error of the radiotelemetry technique was estimated by calculating the mean value and the standard deviation of a distribution of 10 data points acquired with the same equipment, during one minute at the study site. We found that the mean value of the distribution was 0.45 m with a standard deviation of 0.54 m and a maximum value of 1.4 m. The error of the GPS-based technique was estimated from 400 minutes of monitoring the position (one data every 10 minutes) of an individual during the night (the same animal was monitored using the spool-and-line technique to ensure that, during the night, there was effectively no movement). We found that the mean value of the distribution of recorded positions during night with the GPS was 3.15 m with a standard deviation of 3.17 m and a maximum value of 11.25 m.

RESULTS

Maximum daily displacements

We will first show the obtained trajectories of each tortoise using radiotelemetry and GPS-based techniques (see Figs. 3). In Fig. 3 we separated data between seasons: spring 2020 (blue) and summer 2021 (red). The scale of the axes is meters and the starting point of each trajectory was shifted to a common origin of coordinates, the (0,0) point in Figs. 3 (left), that corresponds to the position of the tortoise at the beginning of each day. This graphical representation allows to easily visualize how far a tortoise moves during one day.

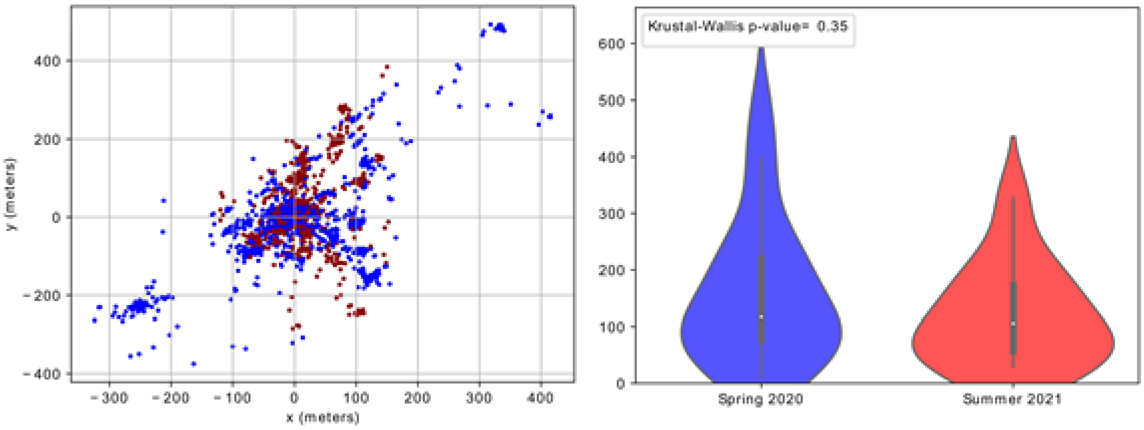

Figure 3. *Left: Estimated positions of the tortoises, relative to a common origin, using radiotelemetry and GPS-based systems during spring 2020 (blue) and summer 2021 (red). For each tortoise, the position at the beginning of the day was shifted to the point (0,0). Right: Distribution of the maximum distance from the starting point for each tortoise and for each day during spring 2020 (blue) and summer 2021 (red).*

As an example, we show in Fig. 4 two trajectories obtained with the GPS-based system corresponding to two different individuals and seasons, a female individual monitored during spring (color progresses from red to white as time advances, see the trajectory on the left of the map) and a male individual tracked during the summer (from light blue to green, on the right of the map).

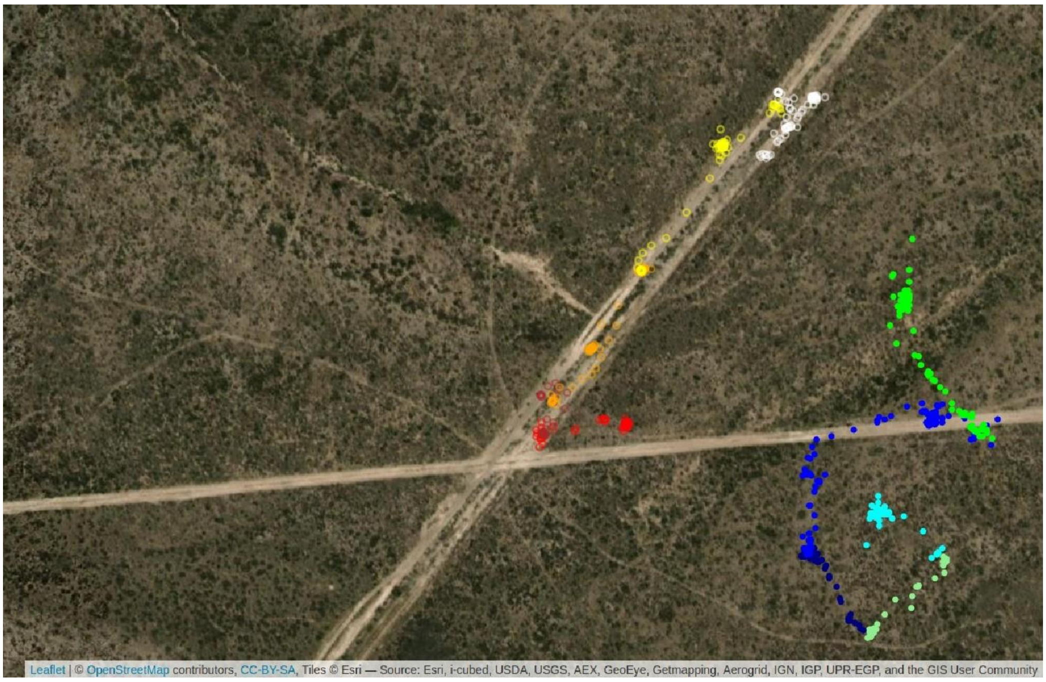

Figure 4. *Two measured trajectories using the GPS-based system for a male individual during spring 2021 (left trajectory, open circles) and for a female individual during spring 2020 (right trajectory, filled circles). Each color represents a monitoring day.*

As a first characterization of tortoises trajectories, we computed the maximal distance from the starting point for each day and for each tortoise, distinguishing between seasons (Fig. 3, right). The mean maximal distance covered was around 110 m. However, the variability of the maximal distance between trajectories was considerably large, varying in a range of more than 400 meters, as can be seen in those figures. We did not find significant differences in the maximum daily distance traveled by tortoises between the seasons.

Maximum visited area

The averaged maximum area visited by each tortoise at the scale of one day was measured as 864 ± 283 m^2 (spring season) and 1034 ± 298 m^2 (summer season; Fig. 5).

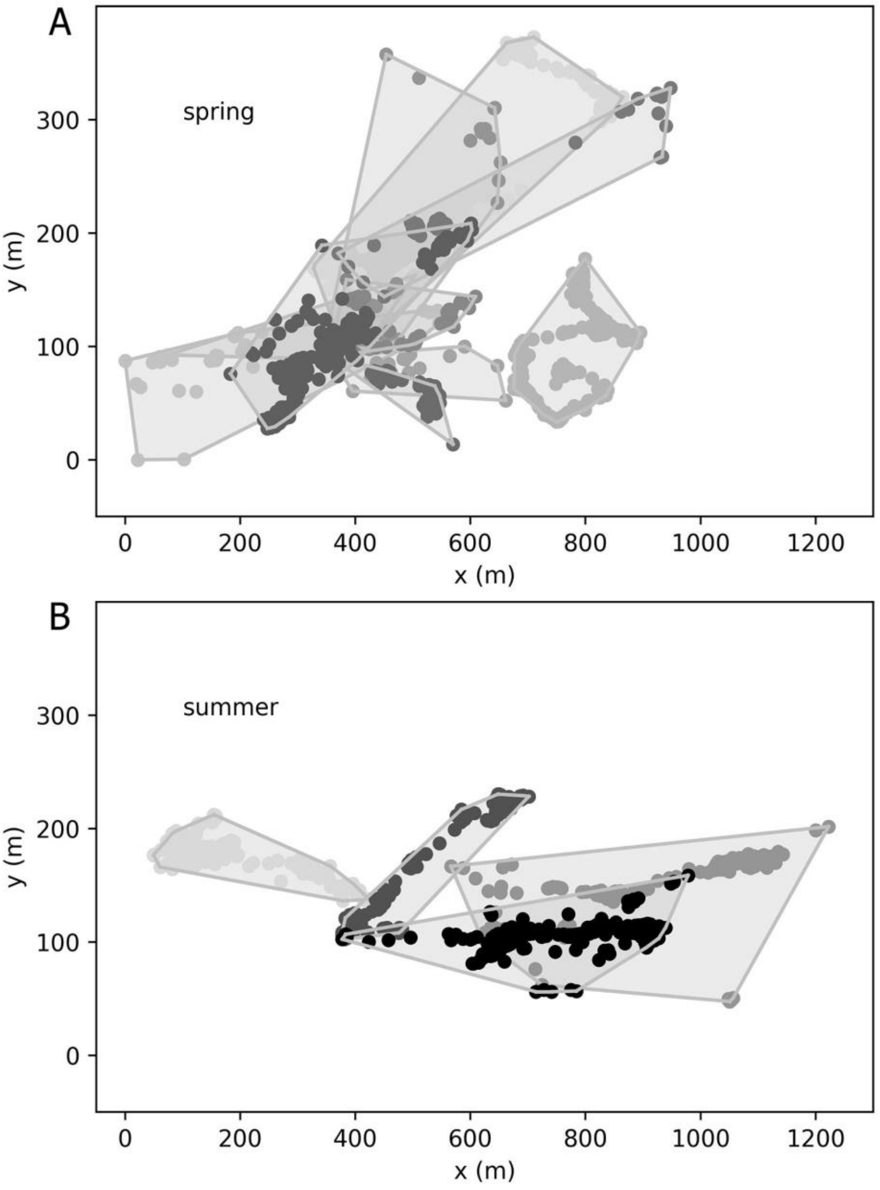

Figure 5. *Convex hulls for the trajectories assessed by GPS-based and radiotelemetry during spring season 2020 (upper panel) and summer season 2021 (lower panel). The shadowed areas constitute a maximum area covered by each tortoise in the corresponding season.*

We found a mostly unimodal distribution of velocity, with a mode of 0.4 ± 0.1 m/min and a median of 0.6 ± 0.1 m/min. Our results show that the movement of these tortoises is subdiffusive, indicating that the balance between perusing their bounded visited region of space and dispersing in the exploration of new space leans towards the former. In other words, the time spent by the tortoise to go from one point to another in space, is shorter than the time spent by a random walker, at least at a daily time scale. Very long steps (of the order of the visited area) are rare, supporting the result that tortoises move inside a bounded region of space. The spatial region in which movement takes place might change every day, but daily movement is performed slower than diffusion.

The trajectories assessed with spool-and line have a much finer spatial resolution to characterize the distribution of turning angles. The distribution of turning angles, assessed from the trajectories measured with the spool-and-line technique during 2020 and 2021 (Fig. 6A, inset), shows that most angles have little deviation from the direct line, which can indicate a clear direction of movement ahead.

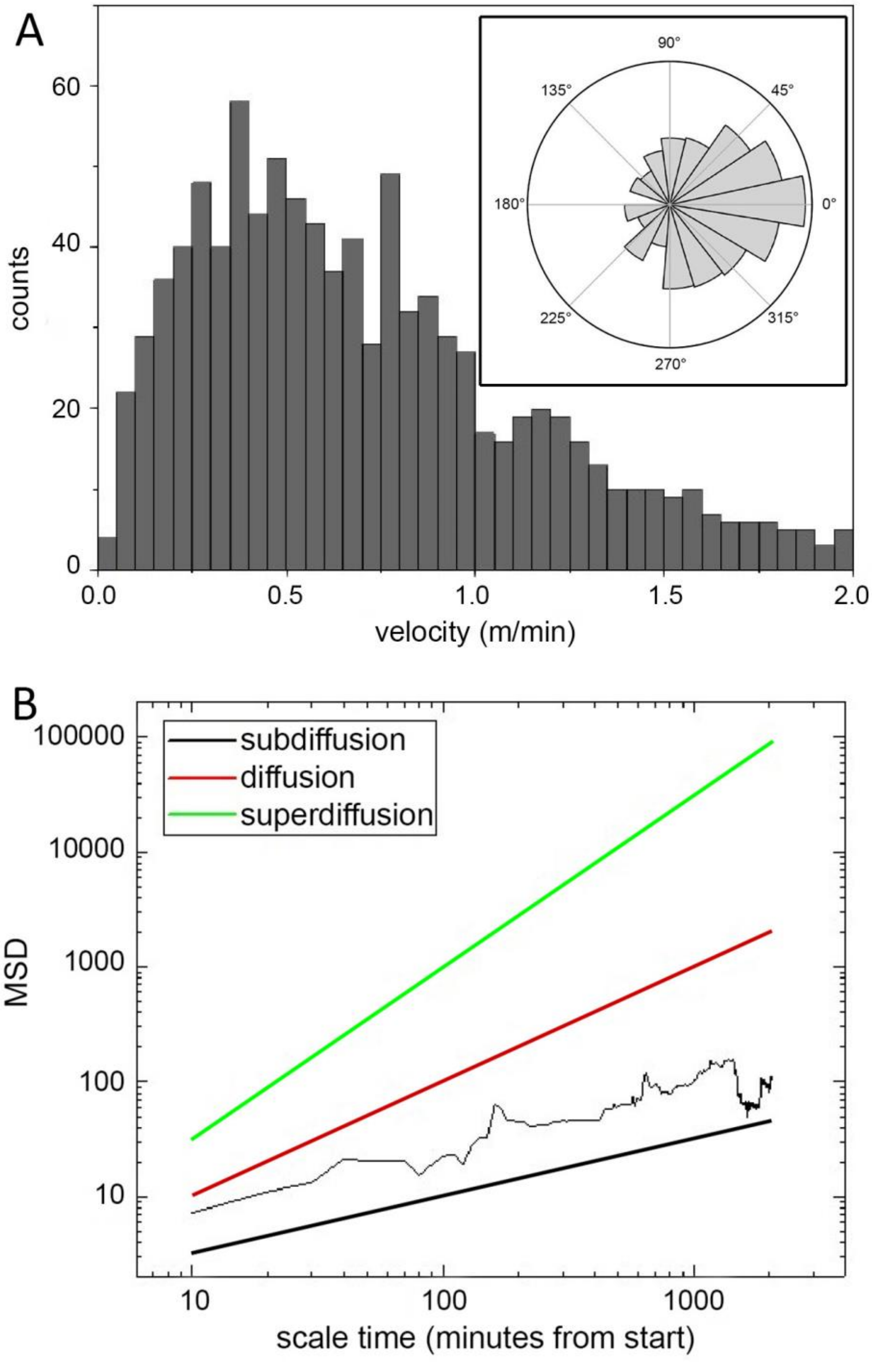

Figure 6. *Characterizations of the trajectories. A) Distribution of the tortoises velocity. The mode of the distribution is 0.4 ± 0.1 m/min and a median of 0.8 ± 0.1 m/min. This distribution is the result of the analysis of data from the GPS-based system placed on 6 individuals (2020) and 4 individuals (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) Mean square displacement (MSD) of monitored tortoises (black thin line), estimated using 2020 and 2021 recorded data with the GPS-based system. Black solid line is shown to guide the eyes and corresponds to a subdiffusive regime, while red and green lines are shown for comparison and correspond to a diffusive and a superdiffusive movement respectively.

CONCLUSIONS AND DISCUSSION

In this work we focus on answering basic questions about the use of space of the species *C. chilensis*: do individuals of this species effectively use a bounded region of space? Does this use really depend on the time of year? These hypotheses, based on observation and were addressed by studying the trajectories of individuals of this species in their natural habitat. For that, we use three complementary techniques that allow to monitor the movement of tortoises: spool-and-line, radiotelemetry and GPS-based system. The spool-and-line technique provided precise trajectories, enough to measure the tortuosity of the walks and it also allows us to ensure that individuals spend the night in one place. While tortuosity could in principle be measured with positions obtained by GPS, the results would be underestimated if the sampling rate is not large enough. Undoubtedly, the data obtained with the spool-and-line technique have better spatial resolution and, therefore, are ideal for measuring tortuosity. It would be of interest to correlate the occurrence of twists with the substrate, at the scale of individual plants. We are currently surveying the vegetation of the field, to address this issue in the near future.

The radiotelemetry and GPS-based techniques allowed us to monitor more than 10 individuals during the spring 2020 and summer 2021 seasons. Using this methodology, we studied the temporal evolution and the properties of their trajectories to test the hypotheses of this work. The spatial and temporal resolution of the GPS data allowed, in addition to determining the speed of movement, to characterize the mean square displacement (MSD). This is a measure of the evolution of the walk as a function of time. The mean of the squared displacements of the present study exhibits a subdiffusive nature of the walks, supporting the hypothesis of the existence of a well-defined bounded region of movement. That sublinear growth (see Fig 9, black thin curve) implies that the tortoises take more time than a random walker to go from one place to another. This can be due to multiple reasons, from the existence of waiting points along the trajectory, to the heterogeneity of the substrate where they walk (Bouchaud and Georges, 1990). As far as random walks are concerned, the subdiffusive behaviour is usually associated with waiting time distributions between steps that have fat tails (Kumar et al., 2010; Metzler and Klafter, 2000, 2004; Klages et al., 2008). However, subdiffusive regimes can be also associated with correlated random walks, for example with memory effects (Bouchaud and Georges, 1990). Behavioural observations should be undertaken in the future to better understand the origin of this relevant result. Regarding the use of the habitat, we found that *C. chilensis* remains within a bounded region of space of 864 ± 283 m^2 (spring season), which expands to 1034 ± 298 m^2 in the summer.

In this work we also seek to answer whether individuals actually move longer distances in the mating season (spring) than in the egg-laying season (summer). Although the medians were not different, in Fig. 3 we observe that greater distances are reached in the spring than in the summer. The results we observed are consistent with the fact that spring is the mating season and both males and females travel to find a mate. However, in the summer it is the females that move the most, especially to find places to lay their eggs. The distance 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, show a negative correlation between carapace length and the average distance that they move per day. On the contrary, the juveniles showed a positive correlation, but males didn't show any relationship between these two magnitudes (Aguirre et al., 1984). In our case, the mean traveled distance did not show differences between males and females despite the marked difference in size (results not shown).

Also, the daily area covered by males during the summer season was similar than the area covered during the summer season (results not shown). However, based on field observations we hypothesize that males show greater daily displacement in spring (mating season) than females in the sense that males are seen to travel long distances to find females to copulate and the opposite occurs in summer (egg laying season). This has been observed in *Gopherus polyphemus* (Daudin, 1802) tortoises, in which case females move more frequently in the summer months and males exhibit a peak in movement during the mating activity (Eubanks et al., 2003) traveling longer distances than females (Guyer et al., 2012). However, to test these hypotheses it will be of importance to have a larger number of monitored individuals to explore significant differences in daily displacements and used area according to sex, size and season. Interestingly we also found that tortoises very often followed the internal trails of the field (see Fig. 4 left trajectory). This behaviour of using open areas for movement also occurs on Galapagos tortoises, which make use of cattle paths, although it was unclear whether these trails were made by tortoises and used by the domestic animals or vice versa (Blake et al., 2021).

Deepening in the analysis of the distances covered, we found that the mean maximal traveled distance is around 110 m in one day, with recorded values of up to 400 meters. These values are compatible with those reported in the (ecologically similar) Mojave desert tortoise *Gopherus agassizii* Cooper, 1863 (Franks et al., 2011). In a radiotelemetry study of the daily movement of this desert tortoise, there were found locations of females ranging from 81 to 354 m, with a mean value of 198 m (Ivanpah Valley, 2000), from 79 to 188 m, with a mean of 132 m (same site, 2001), and from 32 to 130 m, with a mean of 73 m (Fort

Irwin). These distances are also similar in the species of the most phylogenetically related group, the Galapagos giant tortoises, whose daily movements followed more or less 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 experience long-distance seasonal migrations (Blake et al., 2013).

Regarding the speed of movement, we found that *C. chilensis* moves with a most probable velocity of 0.4 ± 0.1 m/min and a median of 0.8 ± 0.1 m/min. The obtained distribution of velocity values can be improved acquiring a higher temporal (e. g. increasing the GPS sampling rate) and spatial (e.g. quantitatively incorporating the information from inertial sensors) resolution of the data. A hint of additional modes of the velocity (which could correspond to different behaviours) can be perceived in the distribution (around 0.8 and 1.2 m/min), but at this stage the available data do not allow to differentiate between different movement modes. For example, the larger velocity mode could be characteristic of a searching mode behaviour, while the smaller one could be an indication of a rambling mode. To go deeper into this hypothesis it would be valuable to complement these results with behavioural observations in the field. In fact, preliminary observations in this regard indicate that, during spring, males seem to spend part of the day walking around, but a considerable portion of the day looking for mates to copulate.

Given the importance to learn about the patterns of movement and habitat use to advance in the development of conservation, restoration and management strategies for this species of tortoise, we believe that our results provide a valuable baseline. For example, one cannot estimate to what extent habitat fragmentation affects this species if we do not assess broad aspects of their basic biology. In the *Monte Austral* ecosystem, near San Antonio Oeste, the main economic activity is extensive cattle ranching. This activity begun to spread in the last 30 years. Therefore, it is relatively new, considering the long life-cycle of tortoises. It is known that cattle produce profound and hardly reversible changes in the vegetation and in the soil of large areas of Patagonia (Paruelo et al., 1993; Borrelli and Oliva, 2001), this compaction of the soil by livestock would cause the destruction of tortoises' shelters and prevent the young from emerging from trampled nests (Waller and Micucci, 1997). In particular, our study site corresponds to an unmanaged field that conserves the ecosystem in a pristine way. Currently, facilities are being prepared to introduce cattle into the area. We do not know how the change in ground and vegetation would affect the movement of this vulnerable tortoise, but our first field campaigns will serve as a baseline to contrast the changes in future years. In the same direction, it is important to evaluate their ecological role as seed dispersers of key shrub species in the biome of the *Monte Austral*. Since the dynamics of the plant population is dependent on the pollination and seed dispersal, it is coupled to the movement dynamics of disperser animals (Morales and Carlo, 2006). In recent years, the number of studies on the role of reptiles in pollination and seed dispersal has increased significantly (Galindo-Uribe and Hoyos-Hoyos, 2007). For example, lizards and tortoises were recently shown to be the most important seed dispersal animals in some areas of the Galapagos Islands (Galindo-Uribe and Hoyos-Hoyos, 2007; Nogales et al., 2017), displaying a larger efficiency than birds in the dispersal of some plant species in a community of the Canary Islands (González Castro et al., 2015).

A related matter is the consumption of fruits by tortoises, which could affect the reproduction of several species of plants and the structure of the vegetation of a community (Stevenson and Guzmán, 2008; Jerozolimski et al., 2009; Richardson and Stiling, 2019). These studies not only demonstrate the ecological importance of tortoises, but also the potential economic role that these animals would have in favoring the reproduction and dispersal of economically important plants (Valencia-Aguilar et al., 2013). In particular, tortoises play important roles in ecosystems, either as prey, foragers, and seed dispersers (Hamann, 1993; Blake et al., 2012). There is still a challenging work ahead in the collection and survey of data, as well as in the analysis and improvement of methodologies to learn more about this vulnerable species. All of these findings could have an important application in the development of measures for the conservation of the species.

Overall, our study highlights the value of using complementary techniques, including our own designed monitoring device, to answer concrete questions about the biology of *C. chilensis*. Moreover, that low-cost and versatile device, created with an open-source philosophy, can be adapted for the use in other related study systems, further enhancing their potential for ecological research.

Data availability

Data and codes are available at: https://gitlab.com/karinalaneri/codestortoisesmovementpaper

Conflict of interest

The authors declare that they have no conflict of interest.

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REFERENCES

Abramson G., Kuperman M., Morales J.M., Miller J.C. (2014). Space use by foragers consuming renewable resources. *The European Physical Journal B* 87:100. doi:10.1140/epjb/e2014-50032-6

Aguirre G., Adest G.A., Morafka D.J. (1984). Home range and movement patterns of the bolson tortoise, *Gopherus flavomarginatus*. *Acta Zoológica Mexicana (ns)* 1:1–28. doi:10.21829/azm.1984.111927

Arfuso F., Cerutti R.D., Scaglione M.C., Sciabarrasi A., Giannetto C., Piccione G. (2022). Evaluation of locomotor activity in female *Chelonoidis chilensis* (Testudinidae, Gray 1870) in response to artificial photoperiod and temperature treatments. *Amphibia-Reptilia* 43:277–285. doi:10.1163/15685381-bja10096

Barton K.A., Phillips B.L., Morales J.M., Travis J.M. (2009). The evolution of an ‘intelligent’ dispersal strategy: biased, correlated random walks in patchy landscapes. *Oikos* 118:309–319. doi:10.1111/j.1600-0706.2008.16936.x

Bartumeus F., Catalan J., Fulco U., Lyra M., Viswanathan G. (2002). Optimizing the encounter rate in biological interactions: Lévy versus Brownian strategies. *Physical Review Letters* 88:097901. doi:10.1103/PhysRevLett.88.097901

Blake S., Wikelski M., Cabrera F., Guezou A., Silva M., Sadeghayobi E., Yackulic C.B., Jaramillo P. (2012). Seed dispersal by Galápagos tortoises. *Journal of Biogeography* 39:1961–1972. doi:10.1111/j.1365-2699.2011.02672.x

Blake S., Yackulic C.B., Cabrera F., Tapia W., Gibbs J.P., Kümmeth F., Wikelski M. (2013).

Vegetation dynamics drive segregation by body size in Galápagos tortoises migrating across altitudinal gradients. *Journal of Animal Ecology* 82 (2):310–321. doi:10.1111/1365-2656.12020

Blake S., Yackulic C.B., Cabrera F., Deem S.L., Ellis-Soto D., Gibbs J.P., Kummeth F., Wikelski M., Bastille-Rousseau G. (2021). *Movement ecology*. Pp. 261–279 in Gibbs J., Cayot L., Tapia Aguilera W. (Eds.), Galapagos Giant Tortoises. Elsevier, Amsterdam.

Bóo R.M., Peláez D.V., Bunting S. C., Mayor M.D., Elía O.R. (1997). Effect of fire on woody species in central semi arid Argentina. *Journal of Arid Environments* 35:87–94. doi:10.1006/jare.1995.0135

Boretto J.M., Cabezas-Cartes F., Kubisch E., Sinervo B., Ibargüengoytía N.R. (2014) Changes in female reproduction and body condition in an endemic lizard, *Phymaturus spectabilis*, following the Puyehue volcanic ashfall event. *Herpetological Conservation and Biology*. 9(1):181–191.

Borrelli P., Oliva G. (2001). Ganadería ovina sustentable en la Patagonia austral: Tecnología de manejo extensivo. Proyecto de desarrollo sustentable de la Patagonia: PRODESAR. Instituto Nacional de Tecnología Agropecuaria EEA Santa Cruz, Río Gallegos, Argentina.

Bouchaud J.-P., Georges A. (1990). Anomalous diffusion in disordered media: Statistical mechanisms, models and physical applications. *Physics Reports* 195:127–293. doi:10.1016/0370-1573(90)90099-N

Boyer D., Miramontes O., Larralde H. (2009). Lévy-like behaviour in deterministic models of intelligent agents exploring heterogeneous environments. *Journal of Physics A: Mathematical and Theoretical* 42:434015. doi:10.1088/1751-8113/42/43/434015

Breder R.B. (1927). Turtle trailing: a new technique for studying the life habits of certain Testudinata. *Zoologica* 9:231– 437. doi:10.5962/p.203744

Burkart R., Bárbaro N.O., Sánchez R.O., Gómez D.A. (1999). Eco-regiones de la Argentina. Administración de Parques Nacionales, Secretaria de Recursos Naturales y Desarrollo Sustentable), Buenos Aires, Argentina.

Cabrera, M. R. (2022). Las tortugas continentales de Sudamérica austral (p. 216). Editorial de la UNC, 2022. ISBN 978-987-707-241-9

Cei J.M. (1986). Reptiles del centro, centro-oeste y sur de la Argentina: Herpetofauna de las zonas áridas y semiáridas. Monografie IV. Museo Regionale di Scienze Naturali, Turin, Italy.

Cunha A.A., Vieira M.V. (2002). Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic forest of Brazil. *Journal of Zoology* 258:419–426.

doi:10.1017/S0952836902001565

Delciellos A.C., Prevedello J.A., Ribeiro S.E., Cerqueira R., Vieira M.V. (2019). Negative or positive density dependence in movements depends on climatic seasons: The case of a neotropical marsupial. *Austral Ecology* 44:216– 446. doi:10.1111/aec.12666

Eubanks J.O., Michener W.K., Guyer C. (2003). Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). *Herpetologica* 59:311–321. doi:10.1655/01-105.1

Famelli S., Souza F.L., Georges A., Bertoluci J. (2016). Movement patterns and activity of the Brazilian snake-necked turtle *Hydromedusa maximiliani* (Testudines: Chelidae) in southeastern Brazil. *Amphibia-Reptilia* 37:215–228. doi:10.1163/15685381-00003047

Franks B.R., Avery H.W., Spotila, J. R. (2011). Home range and movement of desert tortoises *Gopherus agassizii* in the Mojave Desert of California, USA. *Endangered Species Research* 13:191–201. doi:10.3354/esr00313

Fronhofer E.A., Hovestadt T., Poethke H.-J. (2013). From random walks to informed movement. *Oikos* 122:857–866. doi:10.1111/j.1600-0706.2012.21021.x

Galindo-Uribe D., Hoyos-Hoyos J. (2007). Relaciones planta-herpetofauna: nuevas perspectivas para la investigación en Colombia. *Universitas Scientiarum* 12:9–34.

Gatica A., Ochoa A.C., Pérez-Iglesias J.M. (2021). *Herpetology Notes* 14:499–505.

Gibbs J.P., Sterling E., Zabala F.J. (2010). Giant tortoises as ecological engineers: a long-term quasi-experiment in the Galápagos islands. *Biotropica* 42:208–214. doi:10.1111/j.1744-7429.2009.00552.x

Godagnone R., Bran D.E. (2008). Inventario integrado de los recursos naturales de la Provincia de Río Negro: geología, hidrogeología, geomorfología, suelos, clima, vegetación y fauna. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina.

González-Castro A., Calviño-Cancela M., Nogales M. (2015). Comparing seed dispersal effectiveness by frugivores at the community level. *Ecology* 96:808–818. doi:10.1890/14-0655.1

Gottwald J., Zeidler R., Friess N., Ludwig M., Reudenbach C., Nauss T. (2019). Introduction of an automatic and open source radio-tracking system for small animals. *Methods in Ecology and Evolution* 10:2163–2172. doi:10.1111/2041- 468210X.13294

Guyer C., Johnson V. M., Hermann S.M. (2012). Effects of population density on patterns of movement and behavior of gopher tortoises (*Gopherus polyphemus*). *Herpetological Monographs* 26:122–134. doi:10.2307/23325737

Hamann O. (1993). On vegetation recovery, goats and giant tortoises on Pinta Island, Galápagos, Ecuador. *Biodiversity and Conservation* 2:138–151. doi:10.1007/BF00056130

Hunter E.A., Blake S., Cayot L.J., Gibbs J. P. (2021). Role in ecosystems. Pp. 299–315 in Gibbs J., Cayot L., Tapia Aguilera W. (Eds.), Galapagos Giant Tortoises. Elsevier, Amsterdam.

Ibargüengoytía N.R., Kubisch E., Cabezas Cartes F., Fernández J. B., Duran F., Piantoni C., Medina M., Sinervo B. (2020). Effects of acute and chronic environmental disturbances on lizards of Patagonia. Pp. 373–405 in Morando M., Avila L.J. (Eds.), Lizards of Patagonia: Diversity, Systematics, Biogeography and Biology of the Reptiles at the End of the World. Springer International Publishing AG, Gewerbestrasse.

Jerozolimski A., Ribeiro M.B.N., Martins M. (2009). Are tortoises important seed dispersers in Amazonian forests? *Oecologia* 161:517–528. doi:10.1007/s00442-009-1396-8

Kazimierski L., Catalano N., Laneri K., Balazote A., Calzolari G., Joseph J., Amico G., Abramson G. (2021). Trajectory assessment of the vulnerable marsupial *Dromiciops gliroides* in the Patagonian temperate forest. *Mammalian Biology* 101:715–727. doi:10.1007/s42991-021-00106-5

Kazimierski L., Abramson G., Kuperman M. (2015). Random walk model to study cycles emerging from the exploration exploitation trade-off. *Physical Review E* 91:012124. doi:10.1103/PhysRevE.91.012124

Kazimierski L., Abramson G., Kuperman M. (2016). The movement of a forager: strategies for the efficient use of resources. *The European Physical Journal B* 89:232. doi:10.1140/epjb/e2016-70241-1

Kazimierski L.D., Kubisch E., Joseph J., Echave M.E., Catalano N., Abramson G., Laneri K. (2021). Codes and data available from: https://gitlab.com/karinalaneri/codestortoisesmovementpaper.

Kazimierski L.D., Oliva Trevisan A., Kubisch E., Laneri K. and Catalano N. (2023). Design and development of a family of integrated devices to monitor animal movement in the wild. *Sensors* 23:3864. doi:10.3390/s23073684

Klages R., Radons G., Sokolov I. M. (2008). Anomalous transport. Wiley-VCH Verlag, Weinheim, Germany.

Krochmal A. R., Roth T. C. (2023), The case for investigating the cognitive map in non avian reptiles, *Animal Behaviour* 197: 71-80, https://doi.org/10.1016/j.anbehav.2023.01.006.

Kubisch E., Echave M.E., Echave L.A. (2014). *Chelonoidis chilensis* (Chaco tortoise). Predation. *Herpetological review* 45: 684–685.

Kubisch E., Corbalán V., Ibargüengoytía N.R., Sinervo B. (2016) Local Extinction Risk of three species of lizard from Patagonia as a result of Global Warming. *Canadian Journal of Zoology*. 94(1): 49–59. dx.doi.org/10.1139/cjz-2015- 5000024. ISSN: 0008-4301.

Kubisch E.L., Fernández J.B., Ibargüengoytía, N.R. (2023). Thermophysiological plasticity could buffer the effects of global warming on a Patagonian lizard. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*.

Kubisch E., Ibargüengoytía N.R. (2021). Reproduction. Pp. 157–174 in Gibbs J., Cayot L., Tapia Aguilera W. (Eds.), Galapagos Giant Tortoises. Elsevier, Amsterdam.

Kumar N., Harbola U., Lindenberg K. (2010). Memory-induced anomalous dynamics: Emergence of diffusion, subdiffusion, and superdiffusion from a single random walk model. *Physical Review E* 82:021101. doi:10.1103/PhysRevE.82.021101

Lagarde F., Guillon M., Dubroca L., Bonnet X., Ben Kaddour K., Slimani T., El mouden E.H. (2008), Slowness and acceleration: a new method to quantify the activity budget of chelonians. *Animal Behaviour*, Volume 75, Issue 1, 319- 511, ISSN 0003-3472, https://doi.org/10.1016/j.anbehav.2007.01.010.

Law S.J., De Kort S.R., Van Weerd M. (2016). Morphology, activity area, and movement patterns of the frugivorous monitor lizard *Varanus bitatawa*. *Herpetological Conservation and Biology* 11:467–475.

León R.J., Bran D., Collantes M., Paruelo J.M., Soriano A. (1998). Grandes unidades de vegetación de la Patagonia extra andina. *Ecología austral* 8:125–144.

Macdonald L.A., Mushinsky H.R. (1988). Foraging ecology of the gopher tortoise, *Gopherus polyphemus*, in a sandhill habitat. *Herpetologica* 44:345–353.

Mennill D.J., Doucet S.M., Ward K.-A.A., Maynard D.F., Otis B., Burt J.M. (2012). A novel digital telemetry system for tracking wild animals: a field test for studying mate choice in a lekking tropical bird. *Methods in Ecology and Evolution* 3:663–672. doi:10.1111/j.2041-210X.2012.00206.x

Metzler R., Klafter J. (2000). The random walk's guide to anomalous diffusion: a fractional dynamics approach. *Physics reports* 339:1–77. doi:10.1016/S0370-1573(00)00070-3

Metzler R., Klafter J. (2004). The restaurant at the end of the random walk: recent developments in the description of anomalous transport by fractional dynamics. *Journal of Physics A: Mathematical and General* 37:R161. doi:10.1088/0305-4470/37/31/R01

Miles M.A. (1976). A simple method of tracking mammals and locating triatomine vectors of *Trypanosoma cruzi* in Amazonian forest. *The American Journal of Tropical Medicine and Hygiene* 25:671–674. doi:10.4269/ajtmh.1976.25.671

Morales J.M., Carlo T.A. (2006). The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology* 87:1489–1496. doi:10.1890/00129658

Morales J.M., Fortin D., Frair J.L., Merrill E.H. (2005). Adaptive models for large herbivore movements in heterogeneous landscapes. *Landscape Ecology* 20:301–316. doi:10.1007/s10980-005-0061-9

Morales J.M., Moorcroft P.R., Matthiopoulos J., Frair J.L., Kie J.G., Powell R.A., Merrill E.H., Haydon D.T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2289–2301. doi:10.1098/rstb.2010.0082

Morello J., Matteucci S.D., Rodriguez A.F., Silva M.E., Mesopotámica P., Llana P. (2012). Ecorregiones y complejos Ecosistémicos de Argentina. Orientación Gráfica Editora, Buenos Aires, Argentina.

Nathan R. (2008). An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences* 105: 539 19050–19051. doi:10.1073/pnas.080891810

Nogales M., González-Castro A., Rumeu B., Traveset A., Vargas P., Jaramillo P., Olesen J., Heleno R. (2017). Contribution by vertebrates to seed dispersal effectiveness in the Galápagos Islands: A community-wide approach. *Ecology* 98: 2049–2058. doi:10.1002/ecy.1816

Oyarzabal M., Clavijo J.R., Oakley L.J., Biganzoli F., Tognetti P.M., Barberis I.M., Maturo H.M., Aragón M.R., Campanello P.I., Prado D.E., et al. (2018). Unidades de vegetación de la Argentina. *Ecología Austral* 28:040–063. doi:10.25260/EA.18.28.1.0.399

Paruelo J., Bertiller M., Schlichter T., Coronato F. (1993). Secuencias de deterioro en distintos ambientes patagónicos: Su caracterización mediante el modelo de estados y transiciones. GTZ, Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina.

Prado W.S., Waller T., Albareda D.A., Cabrera M.R., Etchepare E.G., Giraudo A.R., González Carman V., Prosdocimi L., Richard E. (2012). Categorización del estado de conservación de las tortugas de la República Argentina. *Cuadernos de herpetología* 26:375–388.

Reynolds A. (2012). Distinguishing between Lévy walks and strong alternative models. *Ecology* 93:1228–1233. doi:10.2307/23213516

Richard E. (1994). Espectro trófico de *Chelonoidis chilensis* (Chelonii: Testudinidae) en la provincia fitogeográfica del Monte (Mendoza, Argentina). *Cuadernos de Herpetología* 8:131–140.

Richard E. (1999). Tortugas de las regiones áridas de Argentina. L.O.L.A., Buenos Aires, Argentina.

Richardson J.C., Stiling P. (2019). Gopher tortoise herbivory increases plant species richness and diversity. *Plant ecology* 220:383–391. doi:10.1007/s11258-019-00921-4

Sánchez J., Alcalde L., Bolzan A.D., Sanchez R.M., del Valle Lazcóz M. (2014). Abundance of *Chelonoidis chilensis* (Gray, 1870) within protected and unprotected areas from the Dry Chaco and Monte Eco-regions (Argentina). *Herpetozoa* 26:159–167.

Smouse P.E., Focardi S., Moorcroft P.R., Kie J.G., Forester J.D., Morales J.M. (2010). Stochastic modelling of animal movement. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2201–2211. doi:10.1098/rstb.2010.0078

Steinwald M.C., Swanson B.J., Waser P.M. (2006). Effects of spool-and-line tracking on small desert mammals. *The Southwestern Naturalist* 51:71–78. doi:10.1894/0038-4909

Stevenson P., Guzmán A. (2008). Seed dispersal, habitat selection and movement patterns in the Amazonian tortoise, *Geochelone denticulata*. *Amphibia-Reptilia* 29:463–472. doi:10.1163/156853808786230442

Tozetti A.M., Vettorazzo V., Martins M. (2009). Short-term movements of the South American rattlesnake (*Crotalus durissus*) in southeastern Brazil. *The Herpetological Journal* 19:201–206.

Valencia-Aguilar A., Cortés-Gómez A.M., Ruiz-Agudelo C.A. (2013). Ecosystem services provided by amphibians and reptiles in neotropical ecosystems. *International Journal of Biodiversity Science, Ecosystem Services and Management* 9:257–272. doi:10.1080/21513732.2013.821168

Varela R.O., Bucher E.H. (2002). Seed dispersal by *Chelonoidis chilensis* in the Chaco dry woodland of Argentina. *Journal of Herpetology* 36:137–140. doi:10.2307/1565820

Viswanathan G.M., Afanasyev V., Buldyrev S.V., Murphy E.J., Prince P.A., Stanley H.E. (1996). Lévy flight search patterns of wandering albatrosses. *Nature* 381:413–415. doi:10.1038/381413a0

Waller T., Micucci P. (1997). Land use and grazing in relation to the genus *Geochelone* in Argentina. Pp. 2–9 in Van Abbema J, New York Turtle and Tortoise Society, WCS Turtle Recovery Program (Eds.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles - An International Conference. New York Turtle and Tortoise Society, Bronx, USA.