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Original Article

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Social networks of threatened Chaco tortoises (*Chelonoidis chilensis*) in the wild

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ABSTRACT

We studied encounters between Chaco tortoises (*Chelonoidis chilensis*) that are in a threatened state of conservation in Patagonia, Argentina, which constitutes the southern limit of their geographical distribution. We monitored six individuals during different behavioural periods of the year (mating, nesting, and brumation), recording 24 344 encounters after tagging the animals with GPS tags. Constructing bipartite networks of burrows and tortoises, in addition to their projections, we discovered a spatial clustering of the burrows. Moreover, our research revealed that as tortoises approach the brumation period they use fewer unique burrows, engage in less burrow sharing, and increasingly favour spending time in their preferred burrow. During the mating and nesting periods some burrows are shared, whereas this was not the case during the brumation period. We studied the daily interactions through proximity-based networks, accounting for the daytime encounters during the different annual behavioural periods. We found the highest network density during the mating period, decreasing to zero, as expected, for the brumation period, when tortoises remain in their burrows during both night and day. Male–male interactions were more probable during the post-brumation and mating periods. Moreover, the number of daily encounters after sharing a burrow for a given night was found to be significant, which could be an indication of social behaviour and memory. Performing numerical simulations, we found that the proximity-based network densities were much higher than expected by chance, which could be attributable to individual selection of preferred sites or could be indicative of social behaviour among these threatened reptiles.

Keywords: social networks; threatened; Chaco tortoises; *Chelonoidis chilensis*

INTRODUCTION

Interactions are essential to the understanding of animal species behaviour, both between individuals and with other species and their environment (Payne *et al.* 2022, Sridhar *et al.* 2023). The representation of interactions by networks, i.e. a collection of nodes with a set of links between them representing these interactions, is an effective tool for gaining insight into the underlying system (Abramson *et al.* 2011, Psorakis *et al.* 2015, Sah *et al.* 2017, 2018, 2019). If the links are defined to be of a social nature, the resulting animal social network is a compact representation of the population and its interactions. Animal social networks are highly diverse, and properties such as connectivity, robustness, and modularity drive the flow of information throughout the network (Brask *et al.* 2021). For instance, knowing how information travels through the network might help us to understand how some infectious diseases propagate, how communication flows, or how a given population might be structured according to social hierarchies (Silk 2023).

Very little is known about the social networks of reptiles and in particular about the interactions of tortoises (While *et al.* 2009, DeRussy *et al.* 2013, Sah *et al.* 2016). Previous studies on desert tortoises investigated the use of burrows through a

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bipartite network model to identify why certain burrows are more popular than others (Sah *et al.* 2016). Recent work on *Gopherus agassizii*, a desert-dwelling species of tortoise, shows that the network of interactions among individuals through the common (asynchronous) use of burrows differs from a random network, in the sense that some burrows are visited with a higher probability than would be expected in a well-mixed population. For that desert species, burrows constitute an important shelter in extreme weather conditions, hence changes in the network structure might be a proxy for the impact produced by human disturbances, such as habitat fragmentation (Sah *et al.* 2016), or might be correlated with survival after translocation (Germano *et al.* 2017).

In the case of *Chelonoidis chilensis*, a threatened species of tortoise widespread in South America (Ruete and Leynaud 2015) that inhabits arid environments, very little is known about their social behaviour in the wild, hence we do not know how much habitat fragmentation affects this species. For instance, compaction of the soil by livestock might affect tortoise shelters (Waller and Micucci 1997). This raises a concern, given that the main economic initiative in the region under study, the southern ecoregion of mountains, plains, and plateaus, is extensive cattle ranching. This relatively new activity began to spread in recent years, and it is known to produce a profound and hardly reversible change in the vegetation and soil of large areas of Patagonia (Paruelo *et al.* 1993, Borrelli and Oliva 2001). Also, the threat to this species has been exacerbated by the introduction of exotic predatory species, such as wild boar (*Sus scrofa*) (Kubisch *et al.* 2014). Therefore, *C. chilensis* was categorized as threatened by the International Union for Conservation of Nature in 2014. The main factors that led to this situation are the reduction, modification, and destruction of their habitat, owing to expansion of the agricultural frontier, and the wildlife trade, because *C. chilensis* is the most trafficked native reptile in the illegal pet market of Argentina (Prado *et al.* 2012). For instance, *C. chilensis* is included in Appendix II of the *Convention on International Trade in Endangered Species of Wild Fauna and Flora* (CITES 2024).

Burrow sharing or the simultaneous use of burrows during periods of inactivity, such as nights or longer periods, has been observed in many species, but less frequently in reptiles (Leu *et al.* 2011). Reptiles are usually ignored in studies of sociality; however, recent studies report complex social behaviour among some lizards (Fox *et al.* 2003, Mason and Parker 2010, Leu *et al.* 2016) and in some populations of tortoises (Wendland *et al.* 2010, Sah *et al.* 2016). In particular, the studied population of *C. chilensis* lives at the southernmost fringe of its global distribution, where climate annual variability, with cold winters and very hot summers, necessitates a brumation period from April to August. Therefore, the main period of activity is constrained to be from September to March, when mating and nesting take place. The study site corresponds to an unmanaged field that conserves the ecosystem in a pristine way, but currently some facilities are being prepared to introduce cattle into the area. Therefore, habitat fragmentation or any other disturbance with a significant impact on social interaction of *C. chilensis* might be critical for the survival of this threatened species at the edge of its geographical distribution.

To explore the interactions among the individuals of this species, usually considered as solitary (Sah *et al.* 2016), we took into account information from both the specimens and their associated spatial habitat. These data were obtained from field observations and spatiotemporal movement data from individuals, gathered for the purpose of the present study as detailed in the Materials and methods section. The data allow us to identify encounters among individuals and sleep locations. Based on these data, we studied bipartite networks for *C. chilensis*, considering both the tortoises and their burrows. A bipartite network is a specific type of network defined by two types of nodes, where links are allowed to connect only nodes of different types; links among nodes of the same type are not meaningful. Bipartite networks are important and widely used, in particular to model interaction between elements along with information about their membership or affiliation (Abramson *et al.* 2011). For instance, in social bipartite networks, one class of node might represent people, while the other class might represent groups to which these people belong (Newman 2003). In our case, we modelled the tortoise population by choosing one type of node to represent individuals and the other type to represent their burrows, in order to explore whether their sleeping habits provide further insight into their interaction patterns.

Additionally, we designed a simple spatial base model considering individuals with random movement in a spatial area equivalent to the one spawned by the data. We performed numerical simulations, detected encounters, and constructed networks that were compared with those built from field data, aiming to understand the mechanisms of interaction.

MATERIALS AND METHODS

The study was carried out in a site of ~25 ha, located ~20 km north of the city of San Antonio Oeste, Province of Río Negro, Argentina, where there is a stable population of *C. chilensis* with a large number of specimens. The area in general belongs to the Monte Austral phytogeographical 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 in particular, 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 (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. Close to the border of the study area, there is the Gran Bajo del Gualicho, a Patagonian plain ≤70 m 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* and several species of the genus *Atriplex*. Scarce precipitation gives an average of ~255 mm in the year, with minor peaks in spring and autumn. Annual average temperature is ~14.5°C, with significant daily thermal amplitudes and a persistence of the west and southwest winds, making the region more arid (Godagnone and Bran 2008). The minimum average temperature is 1°C, and the maximum is 30°C, with extreme recorded temperatures of −11.5°C and 44.6°C (data for 1961–2021 provided by the National Meteorological Service of Argentina).

We tracked six tortoises continuously during a whole year using GPS data loggers (i-gotU GT-120 Mobile Action, Taiwan), recording geographical coordinates every 15 min. The positions were recorded continuously from 06.00 to 22.00 h and from 02.00 to 03.00 h. The equipment was attached to the carapace of each individual using a camouflage tape (@Duck Tape, Real Tree Hardwood Camouflage) to mimic the environment, with the precaution of not leaving any sharp corners, in order to prevent the tortoise from becoming trapped in vegetation. After attaching the device, tortoises were released at the same place where were found. The weight of the equipment never exceeded 10% of the body mass, in order not to disturb the activities of the tortoises.

In this work, we present analysis and results spanning a whole year, involving a total of 20 149 h of recording by GPS data loggers. Those recorded geographical positions corresponded to 813 trajectories from six individuals. The GPS data loggers were charged every 15 days except during the brumation period, when animals were not disturbed and were observed every 2 weeks to check whether they remained brumating at the same location. All recorded trajectories were preprocessed to exclude those corresponding to speeds above a threshold of 15 m/min, assessed as a reasonable maximum speed for the species, according to the empirical distribution of speed presented in the Supporting Information (Fig. S3).

Based on the behaviour of this species, we considered four different behavioural periods throughout the year: the post-brumation period from September to October, the mating period from November to January, the nesting period from February to April when females search for egg-laying locations and individuals look for places to brumate, and the strict brumation period from May to August (Kubisch *et al.* 2023). For each of these periods we constructed a network of encounters between tortoises during the day. This network consisted of tortoise nodes connected by undirected edges if those tortoises encountered each other during the day. The links of this network represented an encounter if two tortoises were detected within a distance of <20 m at a time interval of <20 min. The degree of a tortoise node indicated the number of tortoises encountered by that tortoise, and the thickness of the edge was proportional to the number of encounters between those two tortoises. These networks were built from a total of 24 344 encounters during the day.

We also constructed bipartite networks of asynchronous burrows (see Figs. S2 and S3). The network consisted of burrow and tortoise nodes connected by undirected edges. An edge connecting a burrow with a tortoise node indicated the use of the burrow by the individual. Therefore, the degree of a tortoise type of node indicated the number of burrows used by that tortoise, and the degree of the burrow type of node represented the number of unique individuals that visited the burrow. For these bipartite networks we considered three behavioural periods, because of insufficient burrow data in the pre- and post-brumation periods, therefore we considered the (same) mating period from November to January, the nesting period from February to March, and an extended brumation period from April to October. Networks were generated using the NetworkX library in PYTHON.

RESULTS

The error in the position was estimated by analysing the set of geographical positions recorded during nights, when tortoises showed no movement. This absence of movement was additionally confirmed by means of a cocoon-like thread attached overnight to the carapace of the tortoise and a proximate branch. The average error found for the position was 20 m.

Encounters during the day

The daily period, typically from ~06.00 to 20.00 h, starts when tortoises begin to move according to the GPS signal variability and ends when tortoises attain refuge in a burrow to spend the night.

The encounter networks between tortoises during the day are shown in Figure 1 (upper panel). As can be seen, there is a striking difference in the network structure for the different behavioural periods of the year. From September to October, we observed the highest intensity of male–male encounters. Interactions between males and females were also intense in this period, according to the thickness of the links between them. From November to January, we observed the highest number of links between tortoises. Interestingly, the male individual T10 became connected to all the females in this period, whereas in the previous one, it was connected only with male T54. As shown in Figure 1 (upper panel), the number of connections diminished during the nesting period (February–March) and reached zero during the brumation period (May–August), as expected. In other words, the density of encounters, defined as $2M/N(N-1)$, where M is the number of links and N the number of tortoises, has a maximum in the mating season, as can be seen in Figure 1 (lower panel).

Regarding the type of encounter during the post-brumation period (September–October), when considering the balance between sexes (accounting for potential pairings with four females and two males) and the hours of measurements for each sex, most encounters are male–male, as shown in Figure 2. Meanwhile, male–female encounters appear to be less frequent. This result is consistent with field observations of a larger number of male–male fights during this period (María Eugenia Echave, personal communication).

We found that male–female encounters were equally frequent from September to January. It is expected that there will be considerable male–female interaction, especially during the mating season (November–January).

From November to January and from February to April, a similar but small amount of female–female encounters was observed (see Fig. 2).

Distinct travel patterns between male and female tortoises were observed throughout the year (see Fig. 3). Males exhibited peak travel distances during February–April (21 ± 14) × 10 m/h, significantly outdistancing the females, which covered an average of 36 ± 24 m/h.

In contrast, during the September–October and May–August periods, males travelled 9.1 ± 4.8 and 9.4 ± 5.8 m/h, respectively, while females averaged 2.5 ± 1.3 and 2.2 ± 1.4 m/h.

Bipartite network of burrows and tortoises

In Figure 4, we show bipartite networks composed of burrows (orange circles) and tortoises (males in light blue and females

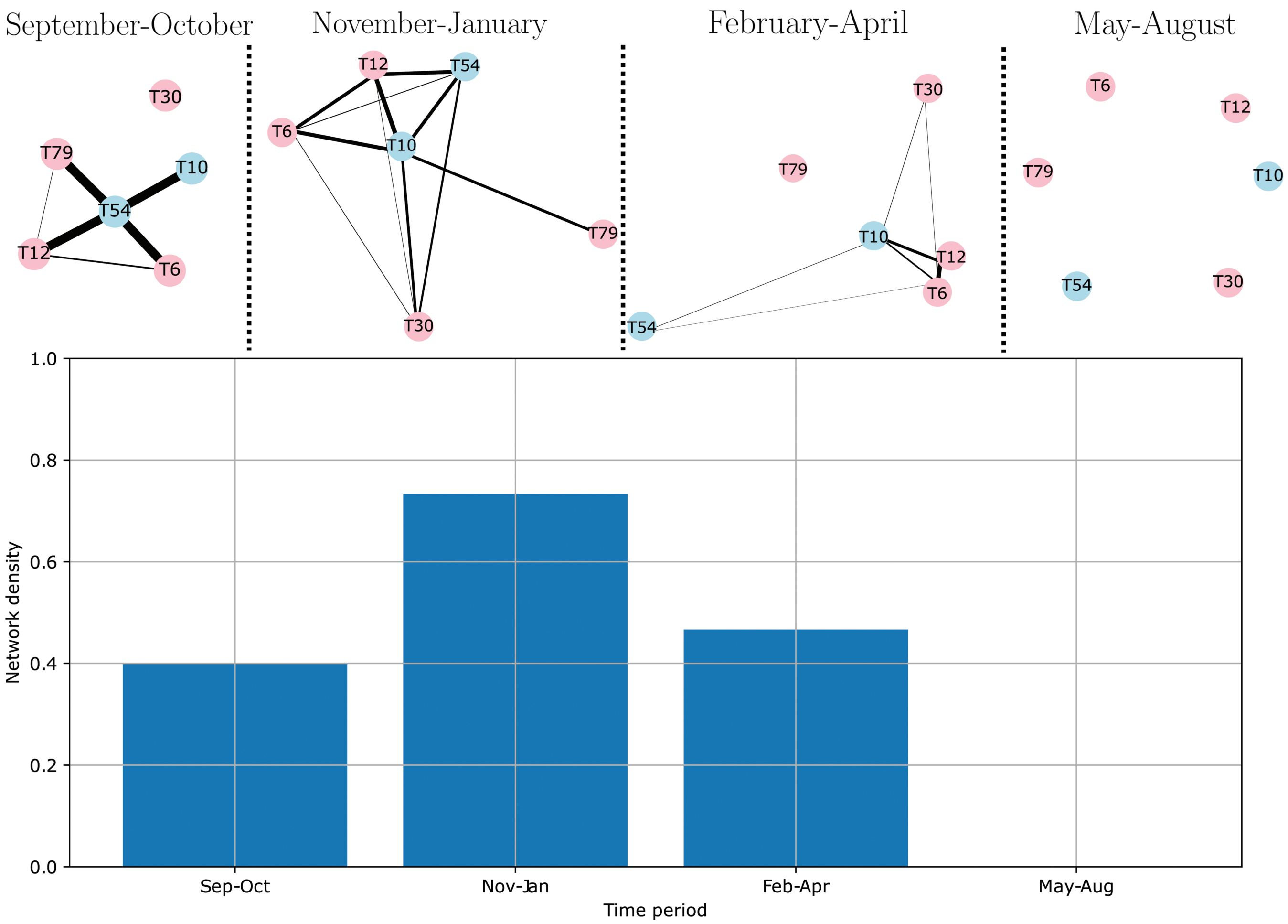

Figure 1. Upper panel, networks of diurnal encounters between tortoises throughout the four behavioural periods of the year. Blue corresponds to males and pink to females. Numbers indicate the individual tortoise identity. Lower panel, network density corresponding to each behavioural period.

in pink). In this type of network, a tortoise is linked to a burrow if the nighttime locations (between 20.00 and 06.00 h) of the tortoise are within a radius of 20 m of the burrow on any particular day. If two tortoises are connected to the same burrow, it is because they used the same burrow, albeit not necessarily at the same time. The thickness of the link is proportional to the number of nights that the tortoise spent in the burrow.

For this analysis, we explored three periods: the mating period (November–January), the nesting period (February–March), and the period immediately before brumation together with strict brumation (April–October). From April to October, tortoises remained brumating in the chosen shelter, and we observed that occasionally, on very sunny days, they went out for sunning during the day and afterwards went back to the burrow to continue with brumation.

At first glance, a striking difference is visible in Figure 4 in terms of connectivity of the network among the three periods. In November–January, during the mating season, some of the tortoises visit a common set of burrows. However, in April, each individual visits its own set, and will finally choose one of them in which to brumate during the winter. It is important to notice that in the bipartite network, burrows are not always occupied by two tortoises simultaneously. Two tortoises might use the same burrow either at separate times or concurrently. Out of 208 distinct measured nights, tortoises were found sharing a burrow on 11 occasions (and only one pair of tortoises for each occasion). We studied the projection of the tortoise network and the projected burrow network further, extracted from the bipartite network.

The network projections of burrows are shown in Figure 5 for the three periods. During the mating season and the nesting or egg-laying season, tortoises sometimes visited a common set of burrows. However, as the brumation period approached (April), each tortoise visited its own set of burrows. Afterwards, each tortoise chose a different burrow in which to brumate during the winter, selected from each set of burrows shown in Figure 5.

We also observed that the number of different burrows used in the brumation period was the smallest. In other words, the mean degree of tortoise nodes in the bipartite network, normalized by the amount of measured hours, decreased as the brumation period approached, as shown in Figure 6. Consistently, the network projection of tortoises (Fig. 7) also showed that the number of shared burrows decreased as the brumation period approached.

We analysed how burrows were distributed in the field and whether burrows connected to each tortoise were close in space.

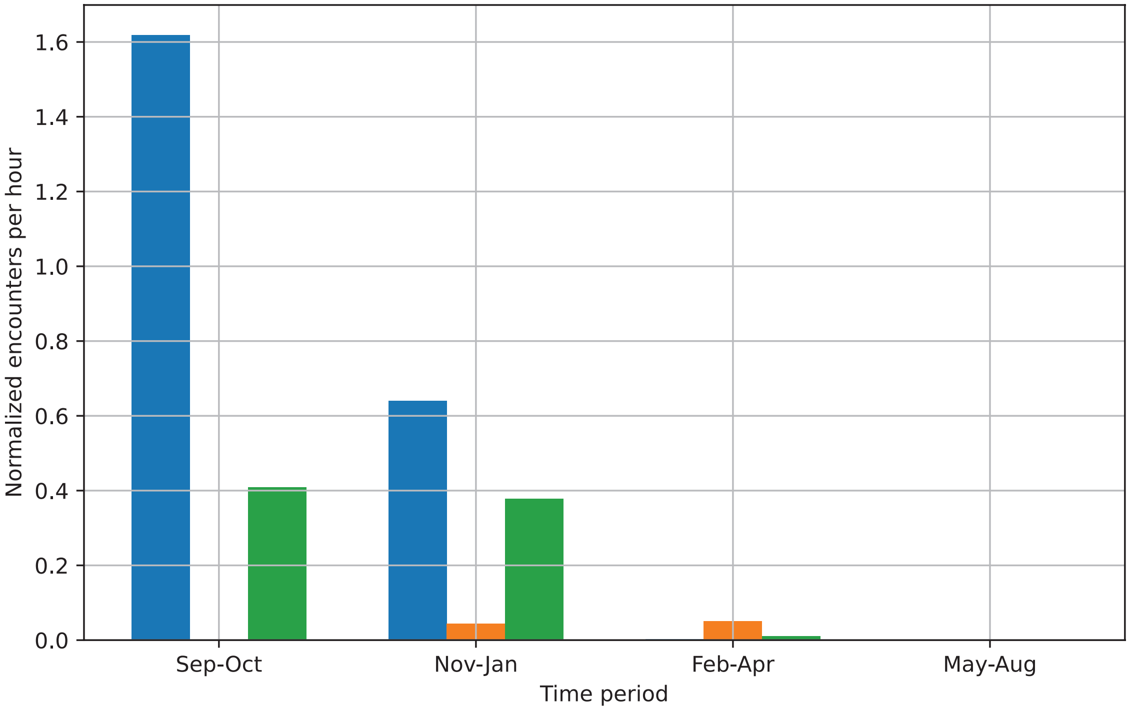

Figure 2. Encounters of type male–male (blue), male–female (green), and female–female (orange) for the four behavioural periods of the year. Counts were normalized by measurement hours for each sex and adjusted for potential pairings (with four females and two males).

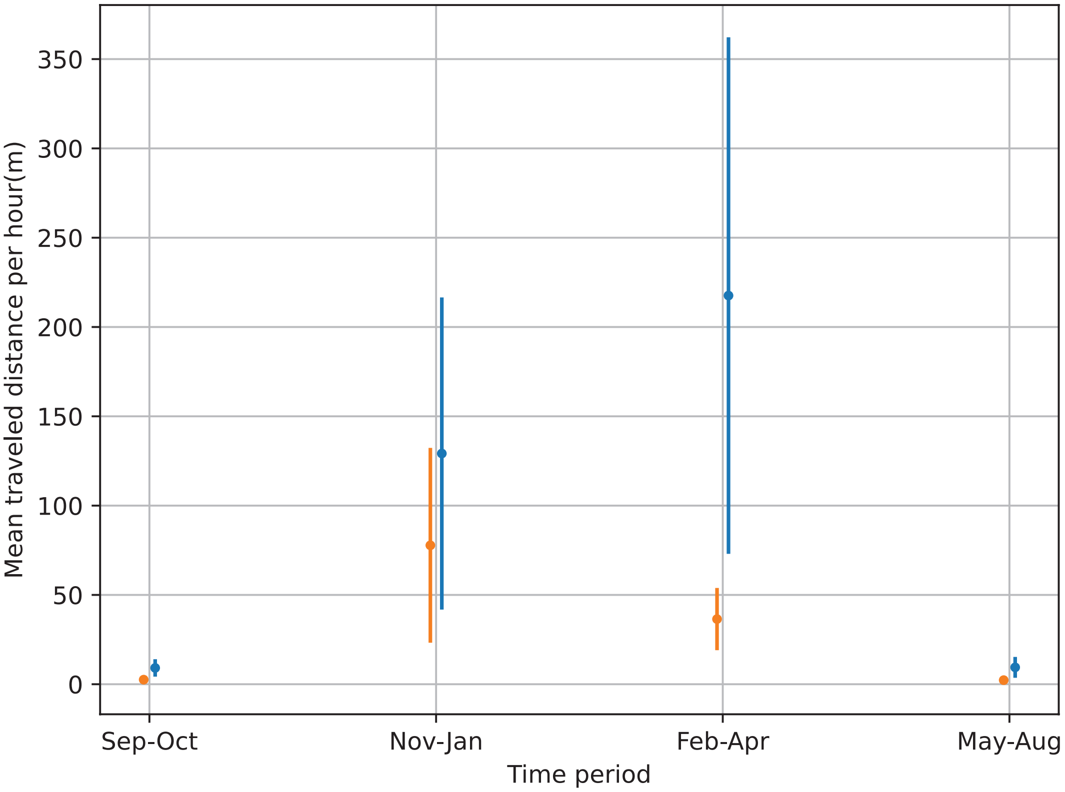

Figure 3. Mean distance travelled per hour for males (blue) and females (orange) for the four behavioural periods of the year.

With that aim, we show the geographical distribution of burrows in Figure 8. In order to quantify this relationship, we computed the adjacency matrix of the projected burrow network (shown in Fig. 5) and its relationship to geographical distances. We used the Mantel test (Mantel 1967) to assess the correlation between geographical distances of burrows and the aforementioned adjacency matrix. The results indicated a significant correlation between both matrices ($P < .05$), suggesting that connected

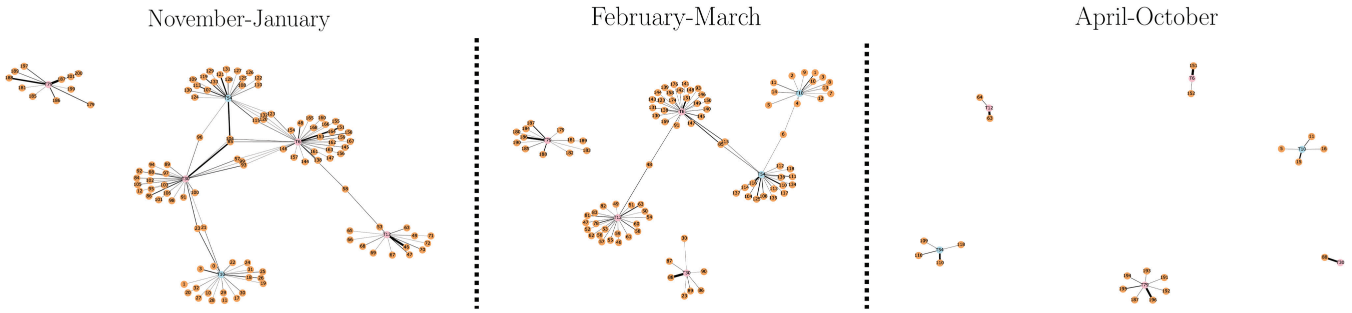

Figure 4. Bipartite network of burrows and *Chelonoidis chilensis* tortoises. Orange circles indicate burrows, blue males, and pink females.

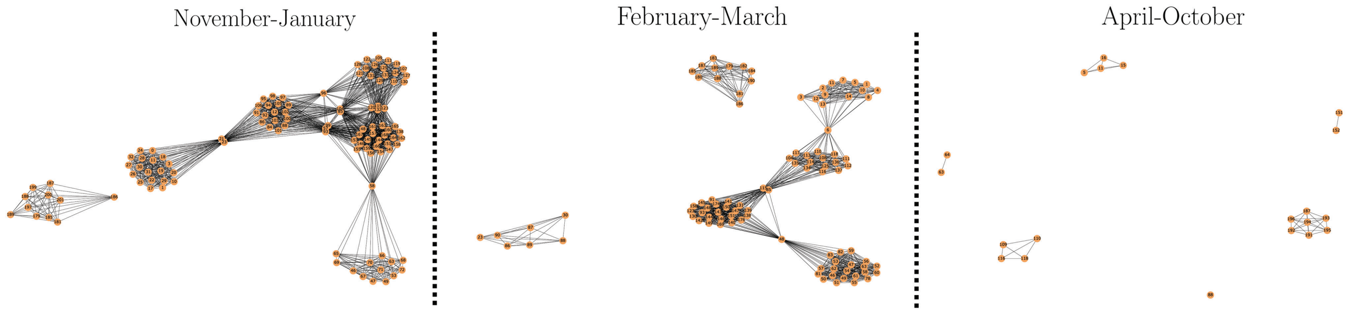

Figure 5. Projected network of burrows (orange), extracted from the network depicted in Figure 4.

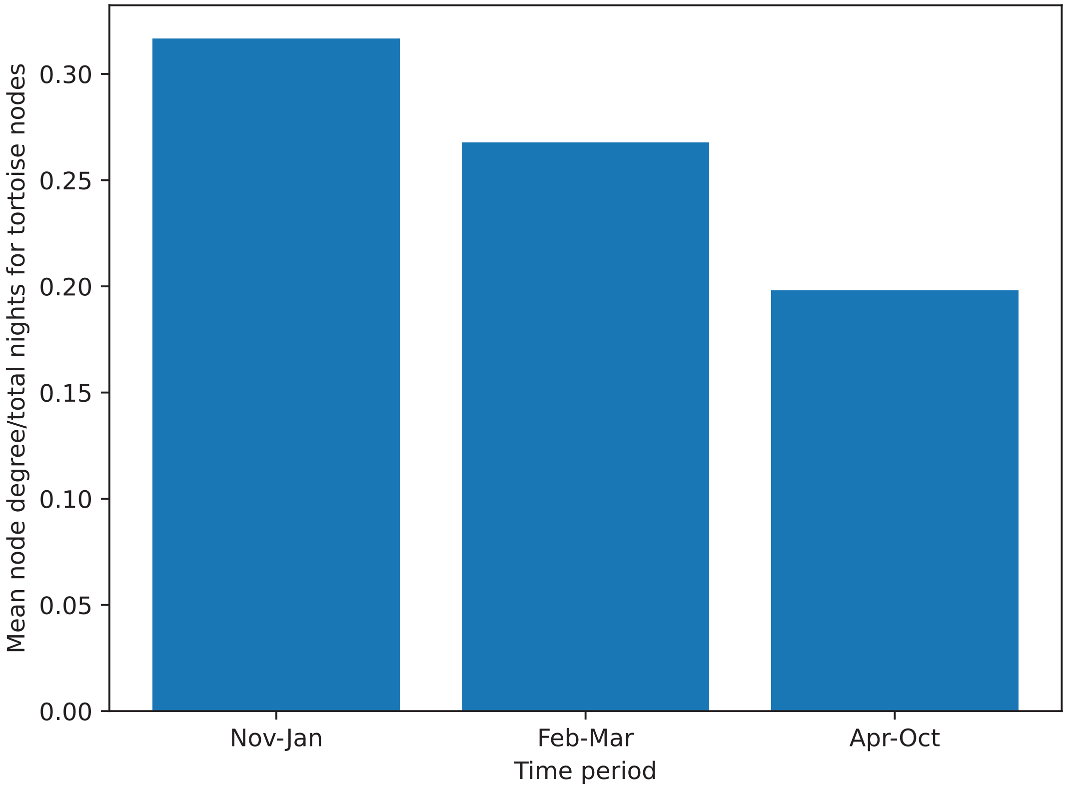

Figure 6. Average degree, normalized by the amount of measured nights, of the tortoise nodes from the bipartite network of burrows for the three periods shown in Figure 4.

burrows in the projection of the bipartite network were, on average, geographically close.

Furthermore, we analysed burrow occupancy to understand tortoise behavioural patterns. We found that, at the beginning of the active season, each tortoise started to use different burrows every night. As the brumation period approached, tortoises spent more and more nights in a preferred burrow, interspersed with occasional nights elsewhere. This predilection appeared

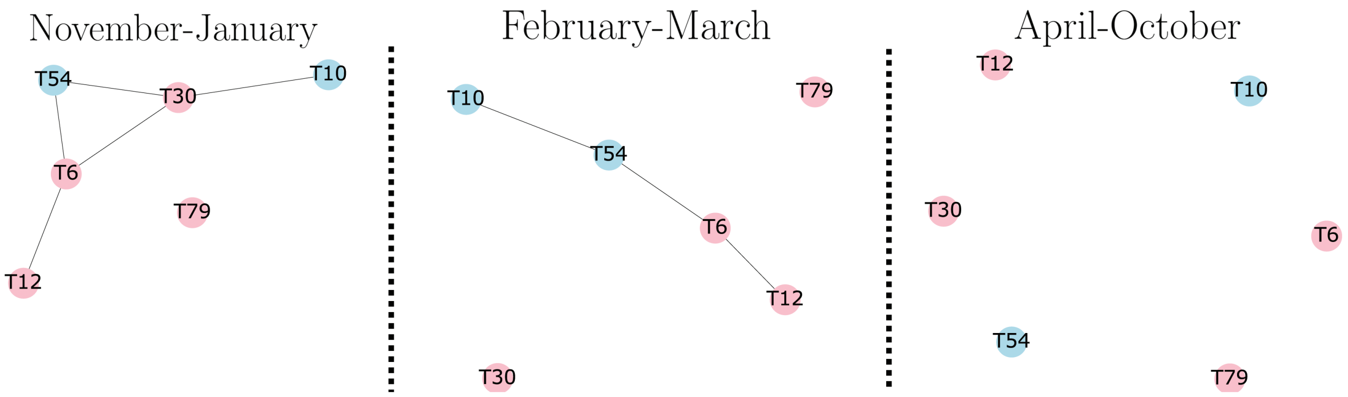

Figure 7. Projected network of tortoises (light blue, males; pink, females) from the network of Figure 4.

Figure 8. Burrows (orange) on the field for the network shown in Figure 4.

to become pronounced towards the end of April, as shown in Figure 9, until they finally chose one of the burrows in which to brumate.

We assessed the geographical position of the most visited burrows (see Supporting Information, Fig. S2). As can be seen in the figure, there were popular burrows that were used much more than others, which were evidently chosen for some quality.

To study the correlation between the simultaneous use of a burrow by two tortoises and a future encounter during the day, we computed the number of those events, as shown in Figure 10. We found that a significant percentage, between 26% and 32.5%, of the encounters during the day occurred after an encounter in a burrow. This could be an indication of a social interaction between tortoises. Encounters, however, do not necessarily imply interaction. It might be the case that tortoises encounter each other by chance during the day; however, a higher rate than chance encounters could point towards social interaction.

To explore this hypothesis, we performed numerical simulations with random walks, with initial conditions consistent with those observed in the field. We ran 1600 realizations of six random walks, using 1080 equal time steps, in a field set to 1 km^2, approximately equivalent to the observed field. The step length was also fixed, determined by the mean value of the empirical speed distribution, shown in the Supporting Information (Fig. S3). After each time step, turning angles were sampled from a uniform distribution between 0° and 360°. These random walk simulations represented a group of tortoises that did not interact with each other. Encounters were identified when points were within 20 m and ≤20 min of each other, following the same criteria as in the field. Subsequently, we generated a synthetic network from each simulation and computed its density, as illustrated in Figure 11.

The observed network densities, displayed in Figure 1 (lower panel), were an order of magnitude higher than the densities

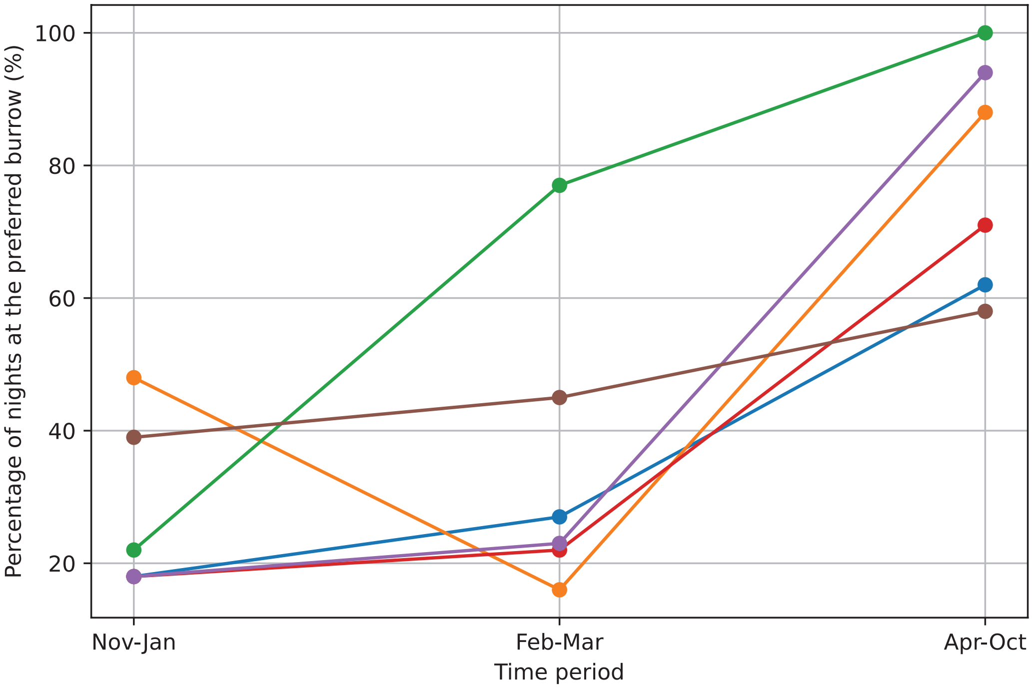

Figure 9. Percentage of measured nights in preferred burrow for each tortoise, segmented by time period. Each colour identifies a different tortoise: green, T30; violet, T6; orange, T12; red, T54; blue, T10; and brown, T79.

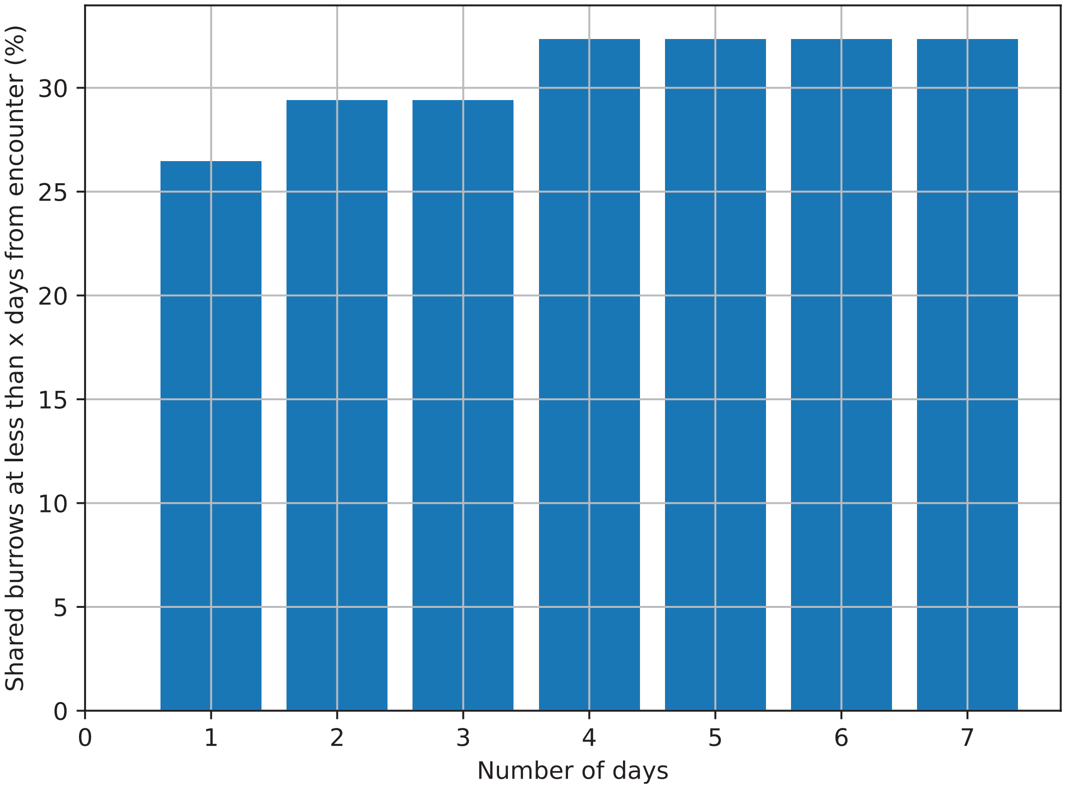

Figure 10. Percentage of burrows shared by tortoises in relationship to the time difference between their occupancy of the same burrow and their subsequent diurnal encounter. Around 30% of diurnal encounters follow shortly (2 or 3 days) after sharing a burrow during the night.

derived from simulations in three of the four behavioural periods, as can be seen in Figure 11. The brumation period was the only instance when a network density of zero was recorded. The differences in network densities between our data and the model suggest that a simple, random walk model does not capture the interactions between individuals. For instance, the densities measured in the field appear to be influenced by additional factors beyond a random walk. Computer simulations that take into

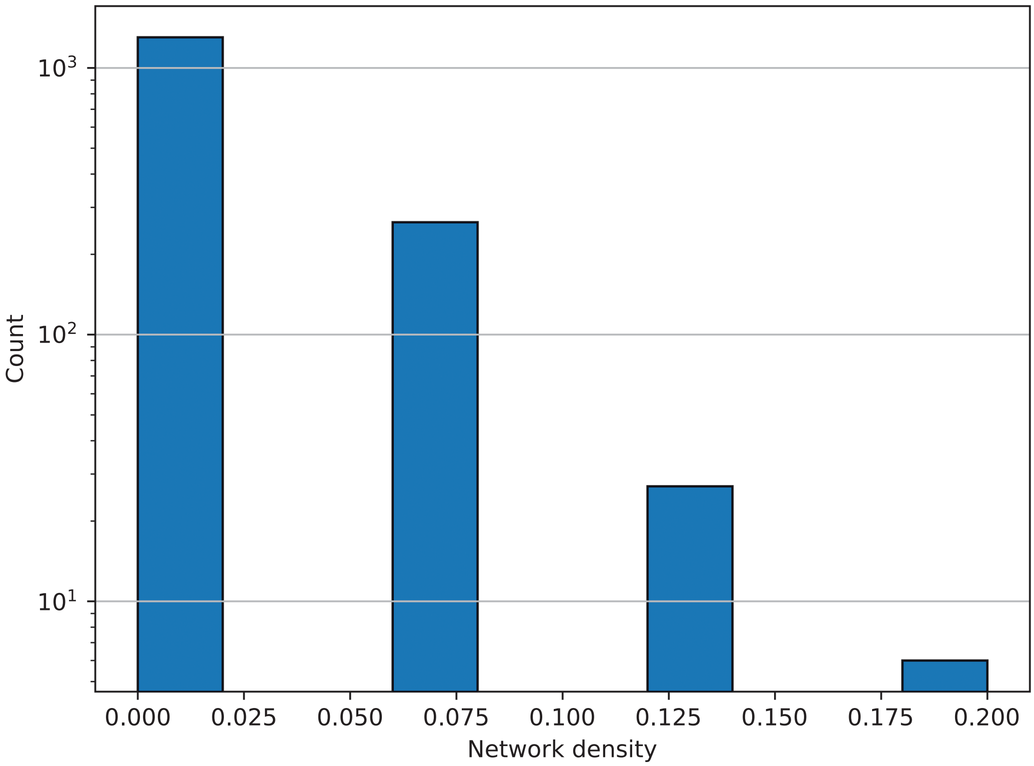

Figure 11. Simulated network densities for 1600 sets of six trajectories in a 1 km^2 field assessed from random walk computer simulations.

account interactions among the individuals (Rubio Puzzo *et al.* 2019, Moreno *et al.* 2020) and their interaction with the environment (Kazimierski *et al.* 2015, 2016) should be performed and compared with data to uncover those additional factors.

DISCUSSION

The knowledge of interactions among tortoises, usually considered solitary, in a population that has not yet been exposed to anthropogenic disturbances, can give us clues about the impact that those disturbances might have in this threatened population. For instance, since the last campaign, two individuals (male tortoise 10 and female tortoise 11) were predated by wild boars (*S. scrofa*). Both were found in a section of the field crossed by a watercourse that is usually dry. Occasionally, when it rains, it fills with water, and wild boars come down to this area to drink. It is presumed that the predation of both tortoises occurred in this way. Given that tortoise 10 was a highly connected male in the social network, its death could strongly affect the social structure of the tortoise population.

We found that *C. chilensis* visited the largest number of different burrows during the mating period, decreasing this number during the nesting season, and reducing to only one burrow as the brumation period approached, in agreement with previous studies on *G. agassizii* populations (Sah *et al.* 2016). We also discovered that the number of shared burrows decreased as the brumation period approached. This finding could be significant in the context of disease transmission among tortoises, which could eventually increase during the sharing burrow period. For instance, some symptoms of upper respiratory tract disease were observed in some individuals. In the future, we will explore the factors that might make certain burrows more preferable than others, such as size, substrate, surrounding vegetation, or orientation of the burrow. Furthermore, burrow popularity is a very important feature that might be indicative of preference, hence monitoring of popular burrows could be important to anticipate population changes owing to habitat fragmentation or other stress factors. Additionally, we observed that connected burrows in the projected bipartite networks were closer in space than other burrows, meaning that tortoises use burrows that are near to each other. This is important to consider when creating a movement model that takes into account the use of burrows.

Regarding the diurnal encounters network, the largest number of connections among all individuals in the monitored community was observed during the mating period, and the lowest number during the brumation period. Concerning post-brumation diurnal encounters, the most probable scenarios involve interactions between males. This is logical because males begin to be active before females and frequently engage in fights with each other. Encounters between males and females are also intense in this period, because of males starting to look for females for mating.

During the mating period (November–January) there is also an increased occurrence of male–male encounters, probably attributable to competition for females. An important number of interactions between males and females are also observed in this period, when males persistently follow females for mating.

The fact that there are more female–female encounters during February could be related to their search for similar areas that meet the ideal substrate and location conditions to lay their eggs. We should explore this result further by intensifying the sampling effort in future fieldwork campaigns, to ascertain whether there is a significant female–female social interaction unveiled by this result.

Our numerical simulations indicate that densities in the diurnal encounter networks are higher than expected from random movements of the population. This suggests that encounters do not occur at random and that there is clear intent behind them.

The distances that some gopher 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* showed 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 did not show any relationship between carapace length and the distance they move per day (Aguirre *et al.* 1984). In our case, average daily walk distances for both males and females of *C. chilensis* increased from small values to higher values during the active season, as expected. Interestingly, males seemed to move on average more than females in the post-brumation period (September–October) and in the nesting period (February–April). After the brumation period we observed in the field that males started to move earlier than females; however, the average distances measured for males were <20 m, which is less than the measurement error. This result highlights the need for further observations in this period.

During the mating period (November–January), we observed similar average distances for both sexes, which is consistent with the observation of males following females for mating. In contrast, between February and April, males seemed to be more mobile than females on average. Although there was a high dispersion in the distance measurement, these results might indicate that interests are different. Females are looking for a place to lay eggs, whereas males might be looking for other resources, such as water or, at the end of April, for a place to brumate.

Interestingly, a significant proportion of diurnal encounters between tortoises took place 1–4 days after sharing a burrow. This fact could be an indication of social interaction and a hint at memory. For instance, during the mating season, copulation has frequently been observed after the tortoises shared a burrow the night before. More behavioural observations will be conducted in the future fieldwork campaigns to assess the type of interaction and its possible relationship to memory. Given that the study region is being modified by the introduction of cattle, it is crucial to gain a better understanding of the social interaction network of tortoises in the wild, in order to design strategies that minimize the impact on this threatened reptile community.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

Dataset: Laneri *et al.*, 2024, TortoisesNetworks, https://github.com/TortoisesSAO/TortoisesNetworks

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