Homing Behavior, Site Fidelity and Territoriality of the Pancake tortoise (*Malacochersus tornieri*) in Kenya

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ABSTRACT

Animals exhibit unique spatial and temporal behaviors that enhance their survival. Understanding such behaviors is an important step towards effective conservation and management especially of threatened species. In this study, we experimented on whether the Pancake tortoise had the ability to home if translocated and also investigated on site fidelity and territoriality of the species in the natural habitats in Kitui County, Kenya. Behavior of 39 tortoises inhabiting 12 spatially separated rock crevices was studied from July 2020 to June 2022 through radio-tracking, camera trapping and combination of group-level scan sampling and ad libitum sampling. Fourteen of the tortoises were fitted with radio-transmitters and trans-located from their respective home crevices to other crevices away from their respective home crevices and their movement and behavior monitored. With an exception of only two females that adapted well to the new crevices of translocation, all the other tortoises attempted homing, with 46.15% of them tracing their way back to their home crevices with accurate precision and 15.38% also reaching areas believed to be within their home range. The successful homing indisputably gives evidence of strong site fidelity in the species. An analysis of the tortoise crevice occupancy showed that there was no statistically significant difference between numbers of the tortoises initially present in the crevices with the average number present over 162 sampling days ($F_{(1,22)}$ = 0.0699, P >0.05), further supporting strong site fidelity in the species. On the other hand camera trapping events and ad libitum sampling also proved the Pancake tortoises to be territorial with males aggressively defending their territories from other incoming males.

Key Words: Animal behavior, chelonian conservation, Ecology, radio-tracking, homing ability.

INTRODUCTION

When individuals display site fidelity, they may attempt to return to their home range following displacement (Ward 2013). This inherent ability by an animal to return home once displaced from a familiar site to an unfamiliar one is called homing (Avens et al. 2003) and is conceived as an aspect of home fidelity (Xiao et al. 2020). Homing behavior has fascinated biologists and lovers of nature alike over the centuries prompting investigations into the mechanisms that make this behavior possible in different animals. Site fidelity, or the tendency of animals to reutilize or return to a previously occupied area has great implication on the animal's ability to access resources that increase their fitness and survival (Giuggioli and Bartumeus 2011). Site fidelity has been traditionally associated to territorialism and other behaviors that result in the emergence of a home range (Switzer 1993; Giuggioli et al. 2006 Borger et al. 2008). Territoriality aims at excluding conspecifics from certain areas through the use of auditory, visual or olfactory signals as well as aggressive interactions (Giuggioli et al. 2011).

Early studies on home range, homing ability, territorial behavior and migration mostly focused on birds, fishes and mammals (Cagle 1944). Over the years, however, notable advances have been made in reptiles, specifically so on site fidelity and homing in sea turtles (Endres et al. 2016). While a handful of studies have investigated on homing and site fidelity in freshwater turtles (e.g. Emlen 1969; Xiao et al. 2020), very few exist on land tortoises, mainly limited to the Herman's tortoise (*Testudo hermanni*) and the Genus *Gopherus*.

A notable study by Chelazzi and Francisci (1979) discovered homing behavior in *Testudo hermanni.* Chelazzi and Delfino (1986) further investigated on the use of olfactory cues by the species during its homing. On Gopher tortoises, Cannor (1996) studied homing in the *Gopherus polyphemus* discovering homing ability in the species but only when displaced over relatively short distances, with higher probabilities of reaching their home range rather than their specific home burrow. More recently, Hinderle et al. (2015) investigated on the effects of homing and movement behaviors on translocation in Agassiz's desert tortoise (*Gopherus agassizii*) in the Western Mojave Desert. Such studies are important as they give insight into how the animals use their environment and thus will inform sound conservation and management strategies for the species (Passadore et al. 2017).

In light of this, we did an investigation on the homing behavior, site fidelity and territoriality of the Pancake tortoise within its natural habitats in Kitui County, Kenya. Pancake tortoise is one of the most thrilling species of land tortoises, with a unique flat morphology and soft shell (Malonza 2003) as well as distinct habitat and behavior. It inhabits rock crevices common in the typical rock outcrop and kopje dominated savannas of Kenya, Tanzania and northern Zambia (Chansa and Wagner 2006). The species is listed in CITES Appendix I and categorized as Critically Endangered in the IUCN Red list of Threatened species owing to declining populations as a result of illegal collection for international trade and habitat loss. Our findings thus bring to light another ecological dimension that has not been studied before but is very necessary for successful management and conservation of the species.

METHODS

Ethics Statement. — The research was done under permission from the Wildlife Research and Training Institute Permit No: WRTI-0104-10-21 and approved by the National Commission for Science, Technology and Innovation (Licence No: NACOSTI/P/22/17049). The study was conducted according to standards for animal health and welfare as stipulated in the National Museums of Kenya ISO certified manual for animal care and humane handling of live animals. No animals were removed from their natural habitats nor their derivatives whatsoever collected.

Study Area. — The study was carried out between July 2020 and June 2022 in Wingemi area, Kitui county, Kenya between 00^{o} - 01^{o} South and 038^{o} - 039^{o} East at an elevation ranging from 510-574m above sea level. The ground here is undulating, generally sandy and has scattered rock outcrops and Kopjes (Kirkpatrick 1997; Malonza 2003) some of which have crevices suitable for Pancake tortoise habitation. The area experiences two rainy seasons: the short rainy season between November and December and long rainy season between March and May. The rains are erratic and thus this region experiences frequent droughts. Rivers and streams are seasonal usually existing as dry river beds. The residents often practice subsistence cultivation and pastoralism.

Combination of Group-level Scan Sampling and Ad Libitum sampling. — Observational sampling methods involving group-level scan sampling and ad libitum sampling as described by Van Belle (2017) were used to study the behavior of 39 Pancake tortoises inhabiting 12 crevices (designated as long-term ecological monitoring stations) in the study area from July 2020 to June

2022. Monitoring visits were made to the stations both during the dry and wet seasons and on each visit the number of tortoises present were recorded. All the activities observed of a given individual or the tortoise family during each visit were recorded. The stations were visited on a rotational basis, usually between 08:00hrs-18:00hrs. Occasional night visits to the crevices were also made to observe the activity of the tortoises at night.

Radio-tracking. — To gather data on movement patterns of the Pancake tortoise, 14 of the tortoises were fitted with R1-2B radio transmitters weighing 9g (Holohil Systems Ltd, Ontario, Canada) between July -December 2020 and their movement tracked using FCC ID: GZ383TTRX1000S radio receiver. Following guidelines by Goodlet et al. (1998), the transmitters were fitted on the front costal (pleural) scute using clear hardened epoxy resin with the transmitter tail positioned slightly facing sideways in females to avoid obstruction during mating. Such kind of transmitters have been successfully used in other chelonian studies without any harm to the animals, for instance the observation on the population ecology of the Three-toed Box Turtle (Rielde et al. 2017).

The first batch of seven tortoises was fitted with radio-transmitters on 26th June 2020. These included three adult male-female pairs and a small adult male that had been residing in the same crevice with a juvenile male. These were fitted with radio-transmitters and translocated in covered boxes from their original crevices and released in two of the crevices (all to the east) designated as long-term monitoring stations: one pair was released at station 1 and the other two pairs and the single male at station 2. The reason for the translocation was to bring the tortoises to accessible crevices for ease of monitoring their behavior. The average distance from the original crevices to the crevices of translocation was 1.37±0.21 km. After one of the translocated tortoises shed off the transmitter, it was collected and fitted to another resident of Station 2, henceforth acting as a control.

Unexpectedly, two of the radio-tracked tortoises started on what seemed to be a westbound homing journey, eventually reaching their respective home crevices, 2.1255km and 1.2798km away, respectively. This unique behavior prompted us to further experiment on the homing ability of the species. We thus collected the two already homed tortoises and released them at a different orientation farther west from their original home crevices to test if the behavior would recur. To increase the sample size, a resident male-female pair of station 4 and another resident male-female pair of station 6 were also collected, fitted with radio-transmitters and interchanged from their respective stations (crevices) on 3rd December 2020. The two stations are 0.523km (straight line displacement) apart, the former on the east and the latter to the west. Additionally, a tortoise pair (a juvenile male and an adult male) from station 11 was also collected, and relocated to Station 2, which is 0.6172km away to the west. All of these tortoises were followed closely to study their movement patterns and behavior.

Figure 1: Radio transmitters tagged tortoises (left), Radio-tracking equipment (middle), camera trap (right)

Camera-trapping. — To help complement the aforementioned methods, and aiming at collecting additional Pancake tortoise ecological information non-invasively and especially at odd hours, four E1C EREAGLE (7.45mm Lens) trail camera traps were deployed close to the rock crevice entrances at station 1, 2, 3, and 5. The cameras were set at video mode so as to collect tortoise behavior and movement near the crevices.

DATA ANALYSIS

Geo-referenced radio-tracking data were analyzed using QGIS software to show the routes followed by homing tortoises and to compute the distances (straight displacement) travelled. Fisher's exact test was used to check if there was a statistically significant difference between those tortoises that homed and those that did not. Crevice occupancy data were analyzed through the Mann-Kendall (MK) test using PAST4.06b software to assess if there was statistically significant upward or downward trends in tortoise crevice occupancy over time. Single factor Analysis of Variance (ANOVA) was computed using Excel, 2013 to compare if there was a statistically significant difference between the tortoise numbers initially present in the crevices with the average number present over 162 sampling days. Examination of videos generated by camera-traps combined with results of behavioral observations further contributed to a better understanding on Pancake tortoise home fidelity, territoriality and other tortoise behaviors.

RESULTS

Homing ability. — (Reference is made to Table 1 and Figure 3) - [n = 13 i.e. total translocations less the tortoise 609HSL[a] that shed off its transmitter at the translocation site and the juvenile 508HSL]. The control tortoise (609HSL[b]) always remained at its home crevice. Two females (976HSL and 627HSL) adapted well to the respective crevices of translocation. Six tortoises, (i.e. three males and three females) representing 46.15% (n=13) of the translocated tortoises traced their way back to their home crevice with exact precision, traveling over an average distance of 1.66km in average of 40 days. When re-translocated to a different orientation, the first two already homed tortoises (910HSL♀ and 942HSL♂) interestingly navigated their way back again to their respective home crevices (across a dry river) covering 0.30km and 1.60km in 1 day and 21 days respectively. The male 527HSL was killed by a predator just 0.23km away from its home crevice, after traveling for a distance of 1.33km in 37 days. Taking the longest distance (0.24km) between two crevices in the study area within which the resident tortoises were observed to freely move back and forth during different seasons, it is assumed that 527HSL had reached its home range. Thus it can be deduced that 8 tortoises 61.54% (n=13) of the translocated tortoises successfully homed covering an average of 2.00km in average of 33.22 days.

The remaining three tortoises (adult males 643HSL and 662HSL and juvenile male 508HSL) attempted homing but failed to reach their respective home crevices. The juvenile 508HSL travelled 0.13km and found a new crevice where it since remained while the male 662HSL had its journey intermittently disrupted by entering into different crevices, one of them inhabited by one female. It shed off its transmitter after 287days having travelled 2.64km. The male 643HSL stopped its homing journey after covering a distance of 4.69km in 39 days. It found a crevice occupied by a male-female Pancake tortoise pair and displaced the male. A day after, the new pair was found mating outside the crevice. Considering the percentages, Fishers exact test showed that there was a statistically significant difference between those tortoises that successfully homed and those that did not home ($X^2 = 5.76$; df = 1, p = 0.021).

Of the tortoises that successfully homed, the female 910HSL traveled the longest distance of 6.092km taking 148 days to reach its original home crevice. Other than 910HSL when re-translocated to a different orientation (homing for 0.3km in less than a day), the female 560HSL traveled the least distance of 0.5164km in three days (Table 1).

The time spent in the crevice of release before beginning the homing differed among the tortoises. While some left immediately after the day of translocation, the male 942HSL tarried for 83 days then started homing. Homing usually happened during daytime although we cannot rule out homing at night as only very limited night-time tracking was done. No tortoise was observed homing in the company of another tortoise. The homing tortoises usually avoided entering any rock crevices on their way and often slept under dead logs, bushes or fences (e.g. fig 2) until they reached their home territories. However, the males 643HSLand 662HSL after several days of homing began to occasionally enter into and out of rock crevices on the way either inhabited or uninhabited by other Pancake tortoises.

Figure 2: Homing tortoise sleeping at the base of a tree

Homing trajectories. — Homing tortoises did not follow a straight line. However, it was observed that individuals that had been collected from the same crevice and released together in another crevice tended to follow similar trajectories moving home (fig. 3). This characteristic movement pattern was remarkable in the tortoise pairs that were interchanged to each other's home crevice i.e. 576HSL♀ and 594HSL♂ (moving westward to Station 4 from Station 6) and 560HSL♀ and 543HSL♂ (moving eastward to Station 6 from station 4). These pairs amazingly crossed paths each travelling the opposite direction.

An exception however occurred for the pair 910HSL♀ and 662HSL♂ (collected from the southwest of the crevice of translocation) whose homing trajectories initially differed. The female first headed west, then seemed to get lost as it turned and moved farther north. This tortoise however took a sharp turn and approached home from the north. On the other hand, the male partner (662HSL), first headed south but after some days changed its course and aligned itself with the track followed by the female 910HSL. The male 643HSL, also collected from the southwest, first moved southward, then turned west and approached home facing north.

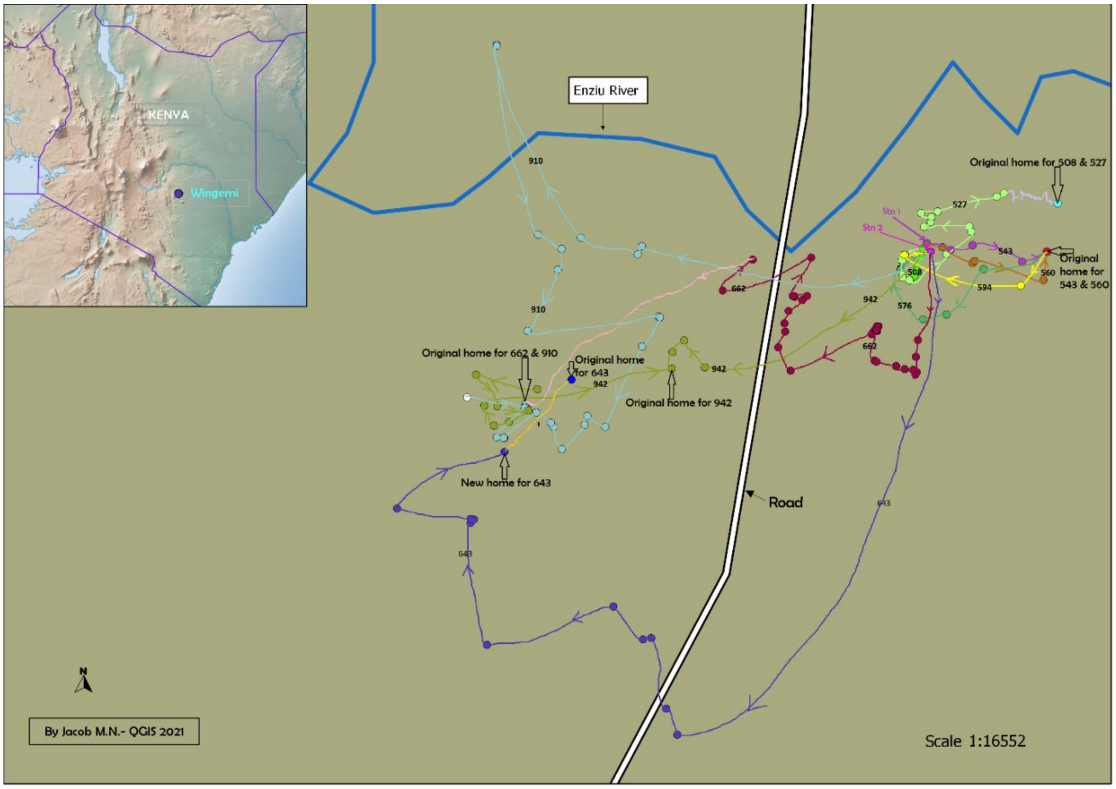

Figure 3: Homing trajectories for radio-tagged tortoises

After successful homing, it was noted that there was a delimited home area, with two or more crevices, within which some of the tortoises could freely reside at different times. Female 560HSL♀, for instance, on its homing journey first entered a crevice (inhabited by another male/female pair) 0.134km south of its original home. Its male partner (543HSL♂) straight homed to their original crevice at Station 6 and after a few days shifted to another crevice on a huge rock 0.088km north of its original home crevice. Nearby there was another crevice inhabited by four other tortoises. 560HSL♀ then eventually moved to the original home crevice and was alone for a day before shifting to the huge rock also inhabited by 543HSL♂. This movement to and fro crevices in the vicinity of the home crevice was also observed for the tortoise 910HSL and 643HSL♂.

Table 1: Radio-tagged Pancake tortoise carapace length, sex, Translocation distances, homing Distances and homing duration

Transmitter no.	**Carapace length (cm)**	**Sex**	**Distance between home and release site(km)**	**Total Distance Traveled (Km)**	**Homing days**
240488-216.609HSL[a]	12	F	0.7555	-	*
240488-216.609HSL[b]	15.3	F	0	0	Control
240491-216.662HSL	15.1	M	2.1255	2.635	287 [δ] *
240498-216.910HSL[a]	14.5	F	2.1255	6.096	148 [†]
240498-216.910HSL[b]	14.5	F	0.302	0.302	1[†]
240500-216.976HSL	15	F	1.2798	0	0 **
240499-216.942HSL[a]	16.2	M	1.284	1.54	70 [†]
240499-216.942HSL[b]	16.2	M	0.47	1.60	21[†]
240490-216.643HSL	12.2	M	1.2798	4.686	39 [δ]
240489-216.627HSL	13.5	F	0.7555	0.052	**
240487-216.594HSL	16	M	0.5232	0.5478	4 [†]
240486-216.576HSL	16.1	F	0.5232	0.9208	10 [†]
240485-216.560HSL	16.9	F	0.5232	0.5164	3 [†]
240484-216.543HSL	15.1	M	0.5232	0.611	5 [†]
240483-216.527HSL	14.4	M	0.6172	1.327	37[φ]
240482-216.508HSL	7.9	M	0.6172	0.131	6 [δ]

NB: items marked (*****) tortoise shed off the transmitter; (******) tortoise never homed (i.e. adapted to crevice / home range of relocation); ([†]) successfully reached home crevice; ([δ]) shows the tortoise ended up in a crevice other than their original homes; ([φ]) tortoise was killed by a predator

Site fidelity. — The successful homing of 61.54% of the translocated Pancake tortoises attests to high site fidelity of the species. Group-level scan sampling, ad libitum sampling and camera trapping further proved that the species exhibits great site fidelity with the tortoises noted to spent over 98% of their time inside their home crevices. Whenever they came out of their crevices, usually during the rainy season, the tortoise spent an average of 34.30±2.52 minutes (n=71 events) feeding and/or mating and always returned to the very crevices. Occasional dry season crevice exit also happened but this was usually by a single tortoise that came out to feed before quickly returning to the home crevice.

Analysis of the Pancake tortoise crevice occupancy by Mann-Kendall test for monotonic trend showed a statistically significant decreasing trend for seven stations (1, 2, 3, 4, 7, 9 and 10) at P<0.001 while for the remaining five stations (5, 6, 8, 9, 11, and 12), there was no statistically significant trend, P>0.05 (Table 2).

Table 2: Analysis of crevice occupancy data by Mann-Kendall test for monotonic trend

Mann-Kendall Test

Station	1	2	3	4	5	6	7	8	9	10	11	12
S :	-2615	-4263	-2253	-2657	-897	-121	-915	-64	-290	-64	-33	-20
Z :	-4.3703	-6.4857	-4.7006	-4.622	-1.7357	-1.6113	-6.8485	-0.6759	-2.9595	-2.4255	-1.6309	-1.3833
p:	1.24E-05	8.83E-11	2.59E-06	3.80E-06	0.082624	0.10711	7.46E-12	0.49911	0.003082	0.015289	0.10292	0.16658

The average Pancake tortoise count in each of the 12 stations over the sampling period covering 162 days across different seasons shows a fairly constant number consistent with the number of tortoises initially present in the stations (Table 3). This is supported by a single factor Analysis of variance (ANOVA) test that showed no statistically significant difference between the number of tortoises initially present in the crevices with the average number present over 160 sampling days, $F_{(1,22)} = 0.0699$, P >0.05, (table 4).

Table 3: Number of tortoises initially present in the crevices and the average over 160 sampling days

Station Number	1	2	3	4	5	6	7	8	9	10	11	12
No. of tortoises initially present	2	2	4	0	5	2	2	2	2	2	2	5
Average no. over 162 days	3.5	4.1	3.6	0.7	4.7	1.0	0.9	1.7	1.8	2.0	0.1	4.0

[NB: It was difficult to count the total number of tortoises in some crevices, especially the deep and narrow horizontal crevices (e.g. station 1, 3 and 5) since the tortoises at the front obstructed our view of the tortoises at the narrow rear part. For instance in station 5 and 6, four tortoises could be visible most of the time but when we eventually extracted them we found a total of six tortoises inside each of the crevices].

Table 4: ANOVA test comparing number of tortoises initially present with the mean number over 160 sampling days

Anova: Single Factor

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
No. initially present	12	30	2.5	2.090909
Mean taken after 162 days	12	28.04461	2.337051	2.465018

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.159315	1	0.159315	0.069937	0.79389	4.30095
Within Groups	50.1152	22	2.277964			
Total	50.27452	23				
Total	50.26998	23				

Territoriality. — Thirteen video events of aggressive behavior were captured in station 2 and 3, with tortoises (identified as males) fighting off other males from entering into the crevice/territory. The fighting bouts involved biting, rigorous pushing and overturning of one another, and as is usual for the Pancake tortoises, righting themselves quickly and then proceeding with the fight. The loser in the fight ran away and the overcomer eventually retained the territory (fig. 4). Besides camera-trapping data, two incidences were observed ad libitum in station 2 and 3 where a male Pancake tortoise aggressively fought back another incoming male from entering into the crevice.

It was noted that while territorial adult males fought other incoming males, females were not aggressive against one another. More than two females (up to five) were observed harmoniously residing with each other in the same crevice throughout the study period. These were in the company of only one territorial male. However, sub-adult males were on two occasions found inhabiting the same crevice with a male juvenile.

Figure 4: Aggressive behavior of male pancake tortoises

DISCUSSION

Homing behavior. —The experiments conducted in this study confirm the Pancake tortoise to exhibit excellent homing abilities. This was attested by the fact that 69.23% of the radio-tracked tortoises that had been displaced from their original home crevices successfully homed. The successful homing again of the first two already homed tortoises when recaptured and re-translocated to a different compass orientation clears any doubt on the existence of homing in the species. Further, the fascinating scenario whereby two pairs of tortoises, collected from and translocated to crevices opposite in direction, crossed paths each journeying home is an allusion to the genius of the homing ability of the Pancake tortoise.

The homing patterns and trajectories imply a response to some cue(s) which at the present cannot be explained with certainty and therefore need further testing. The supposed response to certain cue(s) is evoked by the observation of some distinct movement patterns whereby homing tortoises that had been displaced from the same crevice tended initially to follow the same or nearing paths, only in some cases diverging when nearing their home crevices. We suppose this observed divergence could be as a result of the existence of a wider home range, a delimited area freely traversed by the individual (tortoise) during its normal activities such as feeding, mating, oviposition (Burt 1943).

A number of hypotheses however have been put forward for the mechanisms that make homing possible in animals. Painter and Plachocka (2019) inferring from Mouritsen (2018) and Putman (2018) suggest that for animals to achieve migration, they detect various cues to formulate a map and compass, with the map providing position relative to a target and the compass giving a heading. Such cues include geomagnetic field responses (Brothers and

Lohmann 2015), odour plumes (Koch et al. 1969) and celestial bodies (sun, moon) (Foster et al. 2018).

Even though homing has only been investigated in a few tortoise species, the use of such cues certainly has been documented. Chelazzi and Delfino (1986) state that the Herman's tortoise (*Tesudo hermanni*) makes use of olfaction during homing. Cannor (1996) records that vision and olfaction appear to be important senses for the orientation and movements of Gopher tortoises. Gourley (1974) also records that the Gopher tortoise (*Gopherus Polyphemus*) is capable of making use of sun compass orientation, albeit secondarily to visual landmarks (Cannor 1996). In Pancake tortoise it appears that the response to whichever cue(s) is more perfected in adults than juveniles although it was only one juvenile that was tested. Also, despite our study not investigating further on the cues utilized during the homing, we nonetheless feel that since our tortoises were translocated in closed boxes, the use of visual landmarks by the species may play a lesser role when homing.

Although traveling in incomparable medium with tortoises, Gould (2015) states that Sea turtles memorize the magnetic coordinates of their natal beach, returning to that combination of parameters to lay eggs decades later. To accomplish this feat, Gould (2015) reiterates that the young animal is hypothesized to 'imprint' on the nest site, storing navigational information for later use. Lohmann et al (2001, 2004) explain the global cues used during the homing of Loggerhead sea turtles, as well as juvenile orientation to the initial feeding area, to be unambiguously magnetic.

Site fidelity. — The successful homing of the displaced Pancake tortoises over vast and heterogeneous landscapes is indisputable proof of strong site fidelity in the species. The explanation for the results showing a significantly decreasing trend (Mann-Kendall) is that there were translocations into stations 1, 2 and 4 and consequently the decreasing trend is attributable to the homing movement out of the crevices. Also occasional tortoise dispersals from station 3 to station 4 and back is assumed to have led to decreasing trends in both the stations. The reason as to why there was no statistically significant trend in station 6 despite tortoises having been removed from there is that the tortoises homed within a period (3-5 days) short for a trend to be detected in the long term. 'No trend' in the other stations implied that since there were no translocations out of them, the tortoises initially present remained in the crevices throughout the study period. Considering that reproduction rate in the species is low (Spawls et al. 2002; Schmidt 2006; Mwaya et al. 2018), and our observations that the few hatchlings/juveniles which are reprod uced always find refuge farther away from the adult tortoise crevices, the tortoise numbers in the short term were unlikely to increase hence the constant number in the crevices over the study duration. Our results ultimately show that the tortoises always abided by their crevices and if displaced returned home alluding to strong site fidelity.

These findings agree with Malonza (2003), Wood and MacKay (1997) and Moll and Klemens (1996) who also documented that the Pancake tortoise resides in well-defined home ranges over long periods of time. We believe that such fidelity to the specific crevice and associated habitats certainly confers special survival advantages to the species. For instance, as animals become familiar with a site, site fidelity can help them know where to find good food, nesting sites as well as help them avoid predators (Merkle et al. 2022).

Territoriality. —The camera trap events and ad libitum observations that showed events of aggressive behavior with resident males fighting and chasing away other visiting males add to our knowledge, not only of site fidelity, but also of territoriality. A study by Wood and MacKay (1997) notes that adult males and females of Pancake tortoises may be territorial with respect to other members of their own sex but not to members of the opposite gender. Their observation, further showed that a male may exclude all the other males and a female may do likewise with all other mature females. Our study however did not observe females fighting other females as up to five females were found residing in the same crevice harmoniously for over two years. Since the general habitats surrounding the crevices seem to have comparable vegetation structure and composition, mate territorialism becomes the only reasonable candidate for the aggressive behavior observed.

CONCLUSION

This study provides the first ever information and intriguing evidence on the excellent homing ability of the Pancake tortoise through mechanisms we now can only begin to understand. Further, the study demonstrates the species as exhibiting high site fidelity and territorialism. These ecological findings are important particularly with regard to the development of conservation and management action plan for this critically endangered species. More understanding on the homing behavior is therefore needed for successful establishment of new populations should there arise the need for reintroductions to depleted areas in the future. The subject has implication also for facilities that keep Pancake tortoises in captivity and whose breeding stock is obtained from the wild. In such cases, it is evident that the tortoises have high probabilities of suffering from captivity stresses related to homing especially so if they were collected from the neighboring areas. There is thus need to test the threshold distances over which homing by the species is likely (or not) to happen and to understand the mechanisms that make this behavior possible.

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Declaration of competing interest

The authors declare that there is no competing interests whatsoever in this research.

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APPENDIX 1

Number of Tortoises present in the crevices during each visit

Date	STN 1	STN 2	STN 3	STN 4	STN 5	STN 6	STN 7	STN 8	STN 9	STN 10	STN 11	STN 12
19-06-20	2	2	4	0								
22-06-20	2	2	4	0	5							
23-06-20	2	2	4	0	5			2	2			
26-06-20	2	2	4	0	5							
28-06-20	4	7	3	0	5							
29-06-20	2	6	3	0	5							
01-07-20	4	6	1	0	5							
02-07-20	4	5	4	1	5							
03-07-20	4	5	4	1	5							
05-07-20	4	4	4	1	5							
06-07-20	4	4	4	1	5							
07-07-20	4	4	4	1	5							
08-07-20	4	6	4	1	5							
09-07-20	4	4	4	1	4							
10-07-20	4	4	4	1	4							
11-07-20	4	4	4	1	4							
12-07-20	4	4	4	1	4							
13-07-20	4	4	4	1	4							
14-07-20	4	4	4	1	4							
15-07-20	4	4	4	1	4							
16-07-20	4	4	4	1	4							
17-07-20	4	4	4	1	4							

18-07-20	4	4	4	1	4
19-07-20	4	5	4	0	4
20-07-20	4	5	3	1	4
21-07-20	4	5	4	1	5
22-07-20	4	5	4	1	5
23-07-20	4	5	4	1	5
24-07-20	4	5	4	1	5
25-07-20	4	5	4	1	5
26-07-20	4	5	4	1	5
27-07-20	4	5	4	1	5
28-07-20	4	5	4	1	5
29-07-20	4	5	4	1	5
30-07-20	4	5	4	1	5
31-07-20	4	5	4	1	5
01-08-20	4	5	4	1	5
02-08-20	4	5	4	1	5
03-08-20	4	5	4	1	5
04-08-20	4	5	4	1	5
05-08-20	4	5	4	1	5
06-08-20	4	5	4	1	5
07-08-20	4	5	4	1	5
08-08-20	4	5	4	1	5
09-08-20	4	5	4	1	5
10-08-20	4	5	4	1	5
11-08-20	4	5	4	1	5

12-08-20	4	5	4	1	5
13-08-20	4	5	4	1	5
14-08-20	4	5	4	1	5
15-08-20	4	5	4	1	5
16-08-20	4	5	4	1	5
17-08-20	4	5	4	1	5
18-08-20	4	5	4	1	5
19-08-20	4	5	4	1	5
20-08-20	4	5	4	1	5
21-08-20	4	5	4	1	5
22-08-20	4	5	4	1	5
23-08-20	4	5	4	1	5
24-08-20	4	5	4	1	5
25-08-20	4	5	4	1	5
26-08-20	4	5	4	1	5
27-08-20	4	5	4	1	5
28-08-20	4	5	4	1	5
29-08-20	4	5	4	1	5
30-08-20	4	5	4	1	5
31-08-20	4	5	4	1	5
01-09-20	4	5	4	1	5
02-09-20	4	5	4	1	5
03-09-20	4	5	4	1	5
04-09-20	4	5	4	1	5
05-09-20	4	5	4	1	5

06-09-20	4	5	4	1	5						
07-09-20	4	5	4	1	5						
08-09-20	4	5	4	1	5						
09-09-20	4	5	4	1	5						
10-09-20	4	5	4	1	5						
11-09-20	4	5	4	1	5						
12-09-20	4	5	4	1	5						
13-09-20	4	5	4	1	5						
14-09-20	4	5	4	1	5						
15-09-20	4	5	4	1	5						
16-09-20	4	5	4	1	5						
17-09-20	4	5	4	1	5						
18-09-20	4	4	4	1	5						
19-09-20	4	4	4	1	5						
20-09-20	4	4	4	1	5						
21-09-20	4	4	4	1	5						
22-09-20	4	4	4	1	5						
25-11-20	4	3	3	0	5				1		
26-11-20	4	3	3	0	5				1		
27-11-20	4	2	3	0	5			2	1		
29-11-20	2	2	3	2	5			2			
30-11-20	2	2	3	2	5			2	3		
01-12-20	2	2	3	2	4			2	3		
02-12-20	2	2	3	2	4	2		2	3		2
03-12-20	4	4	3	0	4			2	3		0

04-12-20	4	3	3	0	4			2	3		0	
06-12-20	3	2	3	0	4	1	2	2	3		0	
07-12-20	2	2	3	0	4	1	2	2	2		0	
08-12-20	3	3	3	0	4	1	2	2	2		0	
09-12-20	3	3	3	0	4	1	2	2	2		0	
10-12-20	2	3	2	0	5	1	2	2	2		0	
11-12-20	3	3	2	0	5	1	2	2	2		0	
13-12-20	3	3	2	0	5	1	2	2	2		0	
14-12-20	3	3	2	0	4	1	2	2	2		0	
15-12-20	3	3	2	0	4	1	2	2	2	2	0	
16-12-20	1	3	2	0	4	1	1	1	2	2	0	
17-12-20	1	2	2	0	4	1	2	1	2	2	0	
18-12-20	2	2	2	0	5	1	2	1	2	3	0	
20-12-20	2	2	2	0	4	1	2	1	2	2	0	
21-12-20	3	3	2	0	4	1	2	1	2	2	0	
22-12-20	1	4	3	1	4	1	2	1	1	2	0	
23-12-20	1	4	3	1	4	1	2	1	1	2	0	
24-12-20	3	4	3	1	4	1	2	1	1	2	0	
28-12-20	3	4	3	1	4	1	2	1	1	2	0	
30-12-20	3	4	3	1	4	1	2	1	1	2	0	
31-12-20	3	4	3	1	4	1	2	1	1	2	0	
05-01-21	3	4	4	1	4	0	2	1	1	2	0	5
06-01-21	3	4	4	1	5	1	2	2	2	2	0	
07-01-21	2	4	4	1	4	0	2	2	2	2	0	
08-01-21	3	3		1	4	0	2	2	2	2	0	3

10-01-21	2	4		1	4	0	2	2	2	2	0	
12-01-21	3	4		1	5	0	2	2	2	2	0	
13-01-21	3	4		1	5	0	1	2	2	2	0	
14-01-21	3	4		1	5	0	1	2	2	2	0	
15-01-21	3	4	2	1	5	0	0	2	2	2	0	5
17-01-21	3	4		1	5	0	0	2				
20-01-21	3	4		1	4	2	0	2	2	2	0	
29-01-21	3	3		0	4		0					
01-02-21	4	3	3	0	4		1	2	2	2	0	
02-02-21	4	3		0	4			2	1			
03-02-21		3		0		0		2	1			4
05-02-21	5	3		0			0	2	1	2		
08-02-21	4	3		0	5	7	1	2				5
01-03-21	4	3	3	0	5			2				
04-03-21	6	3	3	0	5			2				
24-03-21	3	3	4	0	5		0	0	1	1		
26-03-21	3	3	3	0	5		0					
29-03-21	3	3		0				0	1			
31-03-21	3	3		0	3	1	0					5
05-04-21	4	3	3	0	5		0					
07-04-21	3	3	4	0	5		0					
08-04-21	6	3	6	0	5		0					
09-04-21	3	2	5	1	5		0					
11-04-21	3	3	4	1	5	1	0					5
12-04-21	3	3	4	1	5		0					

13-04-21	3	3	4	1	5	1						3
14-04-21	3	3	4	1	5	1	0					3
15-04-21	3	4	4	1	5		0					
16-04-21	3	4	4	1	5		0					3
18-04-21	3	4		1	5		0					
21-04-21	3	4		0	5	1	0	2	2	1		4
25-04-21	3	4	4	0	5		0					
04-06-21	3	4	3	0	4	1	0					5
06-06-21	3	4	3	0	4		0					
07-06-21	5	4	3	0	4	1	0					2
08-06-21	5	4	4	0	5		0	2	1	2		4
09-06-21	5	4	4	0	5							
11-07-21	4	4	4	0	5	1						
28-10-21	4	4	3	0	5							
16-11-21	4	3	4	0	5							
Average	**3.5**	**4.1**	**3.6**	**0.7**	**4.7**	**1.0**	**1.0**	**1.7**	**1.8**	**2.0**	**0.1**	**4.0**

Mann-Kendall Test

	STN 1	STN 2	STN 3	STN 4	STN 5	STN 6	STN 7	STN 8	STN 9	STN 10	STN 11	STN 12
S :	-2615.0	-4263.0	-2253.0	-2657.0	-897.0	-121.0	-915.0	-64.0	-290.0	-64.0	-33.0	-20.0
Z :	-4.4	-6.5	-4.7	-4.6	-1.7	-1.6	-6.8	-0.7	-3.0	-2.4	-1.6	-1.4
p (trend) :	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.5	0.0	0.0	0.1	0.2