



Initial orientation and homing performances in the lacertid lizard *Podarcis siculus*

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Homing abilities of lizards after experimental dislocations have been found to be well developed in several species. Following our preliminary findings in *Podarcis siculus*, the present paper reports a new series of experiments on homing performances and initial orientation behaviour upon release. For this purpose, three series of releases were performed at increasing distances from the home areas in which the lizards were captured (range 85–245 m). In each series, two groups of lizards were released: the route-based visual cues during displacement were denied to one of them (NVIS), but allowed for the other (YVIS). The results of initial orientation showed that both are significantly homeward oriented at all three distances tested. Male and female YVIS and female NVIS are similarly homeward oriented, while the male NVIS are not. All 74 lizards successfully returned to their respective home areas. Eleven lizards homed on the same day they were released, while most of them homed during the 1st day after release ($n = 51$) and the rest on the 2nd day ($n = 12$). The different transport treatments did not influence homing success at the different distances tested. These results seem to support the use of a geocentric pilotage strategy to re-enter home from the release spot. Alternatively, the possibility that *P. siculus* use a sun compass and a mosaic map to find their way home is also discussed.

KEY WORDS: homeward heading, geocentric strategy, displacement experiment, visual cue.

INTRODUCTION

It is clearly advantageous for many animal species to have one or more specific places where they can safely rest. This accounts for the fact that natural selection has induced the acquisition of homing capacities for both migratory and sedentary populations (e.g. Gould 2006). This is particularly true for territorial species, given that territory is a precious resource that needs to be established and then defended against conspecific competitors, but entails great effort and energy waste.

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Spatial orientation mechanisms involved in homing behaviour have been investigated in many animal groups (Papi 1992) and especially in birds and arthropods (Papi & Wallraff 1992; Wehner 1992, 2020). It is from both experimental and theoretic studies on these two animal groups that almost all theories and facts regarding strategies and mechanisms derive (Papi 1990; Able 2000; Wallraff 2005; Wehner 2020; Baldaccini 2021).

Reptiles are not among the most studied animals with regard to homing abilities and related orientation mechanisms, notwithstanding the great number of species living in so many ecosystems. Apart from the case of homing in sea turtles (e.g. Lomann et al. 2008), other groups of reptiles also present good homing abilities, as for instance land tortoises, snakes and lizards (Chelazzi 1992). For the latter group, their ability to home across unfamiliar landscapes following experimental dislocations was found to be well developed, even if not ubiquitous, among the different species tested (see the review by Chelazzi 1992 and the subsequent papers by Freake 1998; Jenssen 2002; Huang & Pike 2011; Scali et al. 2013, and references therein).

Following the preliminary findings by Foà et al. (1990), a series of new experiments on *Podarcis siculus* are presented here, with the aim of better depicting not only the homing performances of the species, but in particular their initial orientation behaviour upon release. This important element of the homing process has rarely been considered in herpetological literature. Ellis-Quinn and Simon (1991) and Freake (1998, 2001) measured the bearings of the positions assumed by the lizards at different times (from 30 min to 24 hr) after their release, while the other authors only gathered data on the homing success and did not consider the initial heading of the individuals tested. This information is indeed crucial for understanding what the orientation mechanisms are that enable the lizard to find its way home, unless it is a question of a mere randomly searching for the goal. Consequently, as underlined by Chelazzi (1992), Freake (2001) and Jenssen (2002), while the homing performances of lizards are doubtlessly well developed, their orientation mechanisms are still relatively unknown, except for the well documented use of a time-compensated sun compass (Adler & Phillips 1985; Ellis-Quinn & Simon 1991; Freake 1999; Foà et al. 2009; Beltrami et al. 2010).

With the aim of further enancing the current knowledge on the orientation mechanisms and cues from which the homing abilities of lizards depend, some additional data concerning the influence of the transport conditions on the homing behaviour of *Podarcis siculus* are provided in this paper.

The transport conditions, and thus the role of the outward-journey information on the initial orientation of birds and mammals is a given fact (Wiltschko & Wiltschko 1982; Etienne et al. 1988; Wallraff & Sinsch 1988; Giunchi et al. 2003, and references therein). However their relevance in the case of the short displacements to which lizards were subjected for homing tests are debated. As reported by Freake (2001) transport conditions are crucial in the homing processes of *Tiliqua rugosa*; Jenssen (2002) on the contrary, refuted their role on those of *Anolis cristatellus*.

Podarcis siculus (Rafinesque-Schmaltz 1810) seems to be particularly suitable for studies on initial orientation and homing abilities, according to our preliminary data (Foà et al. 1990). It is a medium sized lacertid lizard widely distributed in Italy (Corti et al. 2011). Both males and females are linked to a stable familiar range of up to 300 m² according to Foà et al. (1990), but see also Mellado and Olmedo (1992) and Avery (1993).

For this purpose, three series of releases were carried out at increasing distances from the home areas in which the lizards were captured (range 85–245 m). In each series two groups of lizards were released: the route-based visual cues during displacement were denied to one of them (NVIS), but were allowed for the other (YVIS). Thus, it is expected that the initial orientation and homing behaviours may or may not support the role of the transport conditions in these processes.

The initial orientation and homing of the two sexes were also evaluated. However, given that they are both linked to a familiar range, there may be no differences regarding their urge to return home or in their initial heading abilities upon release.

MATERIALS AND METHODS

Study site and general methods

The field work was done in the “Tenuta di San Rossore” near Pisa (Central Italy), a part of the Migliarino-San Rossore-Massaciuccoli Regional Natural Park, a coastal wooded area in North-West Tuscany. The 9-ha study area (43°43'25"N–10°18'42"E) is located in a large clearing encircled by an oak-pine forest association dominated by domestic pine (*Pinus pinea*) and ilex (*Quercus ilex*) (Fig. 1). The clearing soil was covered by dry grassland vegetation characterized by a mostly annual (therophytic) species belonging to the *Tuberarietea guttatae* association, but the sandy soil presented occasional patches free of vegetation. Here lizards are widespread, and three main areas in particular host dense populations of lizards because of the presence of suitable refuges (ruined brick floors, low stone walls, wood-piles).

Field observations were made during the summer season of 1991. In June and July, before performing the release experiments, we determined the size of the home range of the lizards to quantify the extent of their familiar area in the study site. To this end, from the same three areas, a total of 18 adult males and 12 adult, non-gravid female lizards were collected at their burrows (or close by) by noosing. Upon capture, each lizard was sexed, snout–vent length measured (SVL), individually colour marked with non-toxic dorsal painting (combinations of dots and letters) and promptly freed, without any dislocation. Each group of lizards from the same area was monitored over the following 8 days. Sightings of these individuals along standard pathways trodden each hour between 8:00 am to 7:00 pm were registered. Their positional fixes were determined in relation to significant elements in the nest areas (clumps of grass, trees, building rubble). Each area was mapped out and reproduced at a scale of 1:50 and the sketch of the mapped area was superimposed against a 50 × 50 cm grid. The resulting mean dimensions of the home ranges are reported in Table 1.

In August, the experimental dislocations and releases took place. Adult lizards (SVL > 50 mm) were trapped by noosing in the same three areas mentioned before and comprised 24 recaptured individuals. In each experimental trial, the trapped individuals were sexed and uniquely colour-marked and then displaced by slowly walking towards a common release point located, respectively, at a distance of 85–105 m westward; at 140–160 m northward; and at 220–245 m north-westward, with regard to the three capture areas (Fig. 1). The dislocation path did not follow a straight line towards the release point, but followed some existing footpaths instead. From the common release point the provenience areas of the lizards were directly visible, since they were all situated at the boundaries of the clearing.

For each trapped individual, the direction of the common release point from their capture site was measured by a hand bearing compass, in order to know their theoretical escape direction (home direction) upon release. The lizards were transported inside small cages of plastic mesh that permit access to any type of sensory information during transportation (YVIS treatment), otherwise the cage was protected by a cardboard cone, open at the bottom, thus preventing any view of the sky and the surroundings (NVIS treatment). The lizards were held about 0.5 m above

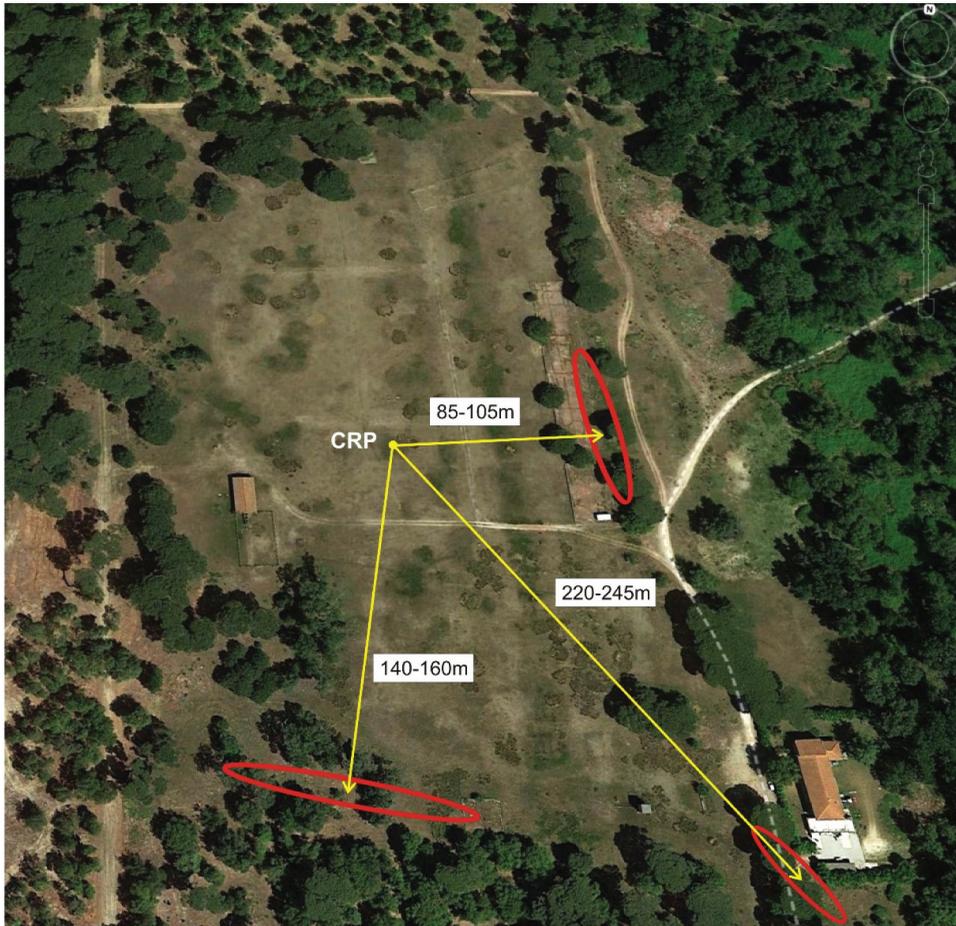


Fig. 1. — A Google Earth image of the clearing where the releases were performed. CRP = common release point. The ellipses mark the areas where the lizards were noosed and the arrows their distance with respect to CRP.

Table 1.

Descriptive statistics of *P. siculus* home ranges at the experimental site of San Rossore, calculated by the minimum convex polygon method (100% of the sightings).

Sex	N	Number of sightings	Home range (m ²)
		mean	mean
Males	18	37.4 (18–48)	216.46 (max 410.94)
Females	12	27.8 (15–48)	155.87 (max 390.30)

the ground during translocation. They were randomly assigned to one of the two treatments, possibly balancing the number of females and males. At the common release point, the cages hung from a wooden platform 1.5 m above the ground, where they remained until release, covered or uncovered according to the transport conditions. Test releases took place on sunny days with no or moderate wind (< 5 m/sec), in the central hours of the day. The lizards were individually released, alternating those assigned to the two treatments, by an operator who gently lowered the cage to the ground via a hole in the platform. The same operator, remaining on the platform, visually followed the lizard until it went out of the circular arena with a radius of 15 m, marked out on the ground. This point was considered the “vanishing point” of any given lizard, and represented its initial heading, the direction of which was registered by a hand bearing compass, together with the time interval needed to exit the circular arena. For circular statistics, the difference between the value of the vanishing point bearing and that of the home azimuth of any given lizard was considered.

The releases of the lizards captured in the 85–105 m area from the common release point (Series A) took place on 4 different days (August 2, 5, 9, 12), those regarding the 140–160 m area (Series B) on 2 days (August 16 and 19), and those regarding the 220–245 m area (Series C) on 2 days (August 7 and 14). The results obtained on each day were pooled for each series.

Any individual was considered as homed when re-sighted at its area of capture, in particular within its previously determined home range or within a 5-m radius around the capture site. To this end, the vicinity of each capture site (uniquely marked by a post) was visually searched for returning subjects during the afternoon (16:00–20:00 hr) of the test-release day as well as on the following days, during which a morning inspection was also done from 10:00 hr to noon. Following this method, it was only possible to verify the return day and the total number of re-entered lizards.

Statistical analysis

The mean vector for each set of bearings was calculated and tested for non-randomness using the V test, by calculating the Homeward component, described by the relation: $H_c = r \cos(\alpha - \sigma)$, where σ = home direction; α = mean vector direction; and r = length of mean vector. Bearing distributions were compared using the Watson U^2 test. To evaluate whether the mean angle of a given sample significantly deviated from the direction of its home area, the confidence interval for the mean angle was used (Batschelet 1981). All statistical analyses were performed in R 4.0.3 (R Core Team 2020).

RESULTS

Initial orientation

Figs 2 and 3 summarize the initial headings of the lizards from the common release point. The mean bearing distributions, obtained by setting the home directions at 0° , of both the YVIS and the NVIS were significantly oriented in all three Series A–C (Fig. 2). In all these distributions, the home direction was included in the 95% confidence interval of the mean direction. The values of the homeward component for the NVIS distributions are nevertheless minor with respect to those of the YVIS. The same is true when the values of the length r of the mean vectors are considered. The distributions of YVIS and NVIS lizards are statistically different in Series B, but not in the other two. The mean time the lizards took to go outside the 15 m arena was shorter but not significantly so for the YVIS with respect to the NVIS in all three series (Series A: $5'48'' \pm 8'38''$ vs $6'21'' \pm 7'09''$; df 16,18; $t = 0.21$, $P = 0.84$. Series B: $3'18'' \pm 3'19''$

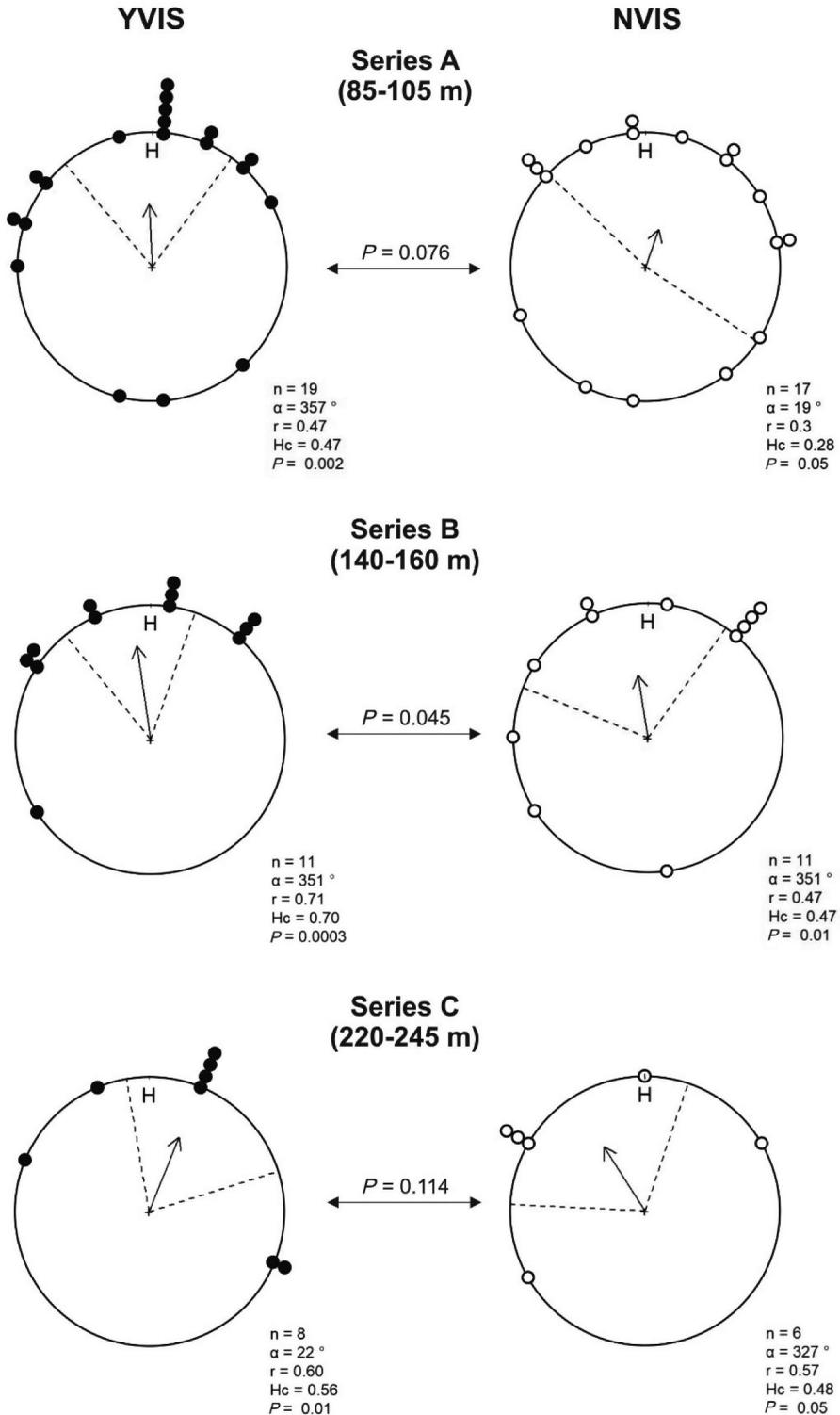


Fig. 2. — Heading distributions relative to home direction set at 0° of lizards displaced at increasing distances from their familiar areas (Series A–C), either with full access (YVIS, left) or no access (NVIS,

vs $5'40'' \pm 4'40''$; df 10,10; $t = 1.37$, $P = 0.19$. Series C: $5'22'' \pm 3'14''$ vs $9'51'' \pm 13'33''$; df 5,7; $t = 0.79$, $P = 0.46$).

The bearing distributions of male and female YVIS and NVIS in the three series, respectively pooled together with respect to their home directions set at 0° , are presented in Fig. 3. Male and female YVIS were found to be homeward oriented, with distributions that were not statistically different. The distributions of the NVIS lizards were also not statistically different, but, while the females were homeward oriented, the males tended to be more dispersed.

Homing performances

All 74 (42 male, 32 female) released lizards successfully returned to their respective home areas (Table 2). A total of 11 lizards were able to home the same day they were released, while the bulk of both the YVIS and the NVIS treated lizards homed the day after release ($n = 51$). The remaining 12 lizards homed during the 2nd day after release. The different transport treatments do not seem to have influenced the homing success at the different distances tested.

Table 3 reports the homing performances of the male and female lizards in each test, irrespective of the transport treatments. The two sexes seem to behave in a rather similar fashion, with comparable homing abilities.

DISCUSSION

Initial orientation behaviour

The initial orientation behaviour is the most original result we have obtained, revealing that already at a short distance from the release site, lizards head in a homeward direction, as suggested by our preliminary report (Foà et al. 1990). Homeward related distributions of “vanishing” bearings of both YVIS and NVIS lizards were obtained at all distances, which suggests that: (i) notwithstanding the stress induced by noosing and other handling, lizards are still capable of homeward orientation upon release; (ii) The transport conditions do not seem to significantly impair the homeward heading ability of NVIS lizards.

YVIS lizards were able to determine the direction of displacement by maintaining continuous visual contact with landmarks characterizing their familiar area, but the NVIS ones were prevented from doing this because of the cone that covered their cages. Compared to the YVIS lizards, this situation may have influenced their emotional status, inducing a worse even if not significant quality of their initial heading and the longer time taken to leave the circular arena. The influence of emotional factors on the initial orientation was also shown in homing pigeons (Del Seppia et al. 1996; Luschi et al. 1996).

right) to visual route-based cues. The mean vector (α) of the sample (n) is represented by an arrow, whose length (r) is drawn relative to the radius of the circle = 1. Hc = Homeward component. Broken lines indicate the 95% confidence intervals. Probability according to the V test. The double-headed arrows between the circular distributions indicate the probability under the Watson U^2 test.

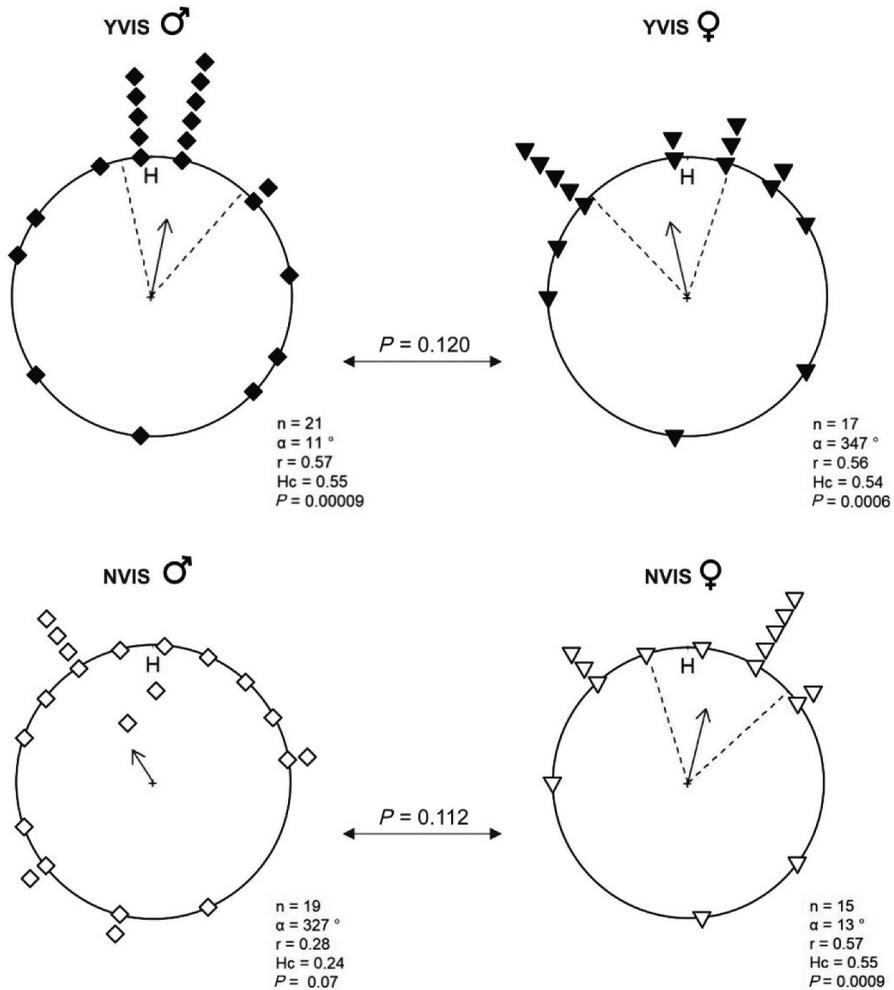


Fig. 3. — Pooled heading distributions relative to home direction set at 0° of male (left) and female (right) lizards in the three series of releases, according to the transport conditions (YVIS top; NVIS below). Further explanation as in Fig. 2.

The fact that homing times of NVIS overlap with those of YVIS lizards suggests that the NVIS treatment effect is limited, influencing only the initial orientation of the lizards within the circular arena.

In the case of YVIS lizards, no differences in initial orientation between sexes were found, both sexes demonstrated comparable homeward orientation. Moreover, the female NVIS and YVIS lizards' performance in homeward orientation was similar. Instead, the male NVIS, on the whole, produced a non-oriented distribution, which is quite surprising and probably due to a stochastic event.

Table 2.
Homing performances of YVIS and NVIS treated lizards in the three release series.

Series	Treat.	Same day n (%)	1 day after n (%)	2 days after n (%)
A	YVIS	1 (5.2)	14 (73.7)	4 (21.1)
	NVIS	3 (15.8)	14 (73.7)	2 (10.5)
B	YVIS	3 (27.3)	8 (72.7)	–
	NVIS	3 (27.3)	8 (72.7)	–
C	YVIS	1 (12.5)	4 (50.0)	3 (37.5)
	NVIS	–	3 (50.0)	3 (50.0)
Total		11 (14.9)	51 (68.9)	12 (16.2)

Table 3.
Homing performances of males and females in the three release series, irrespective of the treatment.

Series		Same day n (%)	1 day after n (%)	2 days after n (%)
A	Male	2 (9.1)	15 (68.2)	5 (22.7)
	Female	2 (12.5)	13 (81.3)	1 (6.2)
B	Male	4 (33.3)	8 (66.7)	–
	Female	2 (20.0)	8 (80.0)	–
C	Male	1 (12.5)	5 (62.5)	2 (25.0)
	Female	–	2 (33.3)	4 (66.7)

Homing performances

In the present study all the displaced individuals returned to their familiar areas, regardless of the distances at which they were released, their sex or the treatment during dislocation. This result prompts us to think about the possible homing capability of *P. siculus* even from longer distances, which so far have not been tested.

Diurnal lizards are very active animals, structurally capable of sudden springs and fast locomotion for monitoring and interacting with preys, predators and conspecifics or in search of a putative sexual partner (Avery 1993; Miles et al. 2000), and indeed rely on acute eyesight (Fleishman 1992). The range of lizards' movements could be seasonally enlarged, inducing the knowledge of sites other than those surrounding their home ranges. It would be reasonable to expect that an extension of known landmarks, would facilitate homing opportunities, as hypothesized for some iguanids species and for *P. muralis* as well (Spoecker 1967; Ellis-Quinn & Simon 1989; Scali et al. 2013).

The absence of differences in homing performances between YVIS and NVIS lizards strongly suggests that cues gathered during transportation do not influence the ability or speed in returning home. Moreover, returning to a specific area from a distant release site strongly indicated the relative importance of a familiar home range to fitness by both sexes.

As regards behaviour upon release, lizards respond promptly by rapidly escaping the arena circle. In this manner they cover a significant part of the return path, particularly in A Series. A question can be posed: why was the actual re-sighting at familiar areas delayed so much? It could be because even if lizards homed rapidly, they remained sheltered and undetectable in their refuges, perhaps due to the stress of transportation and handling. This issue may be resolved in the future by using radio-telemetry devices.

What orientation strategy for P. siculus?

The present results show that *P. siculus* is able to re-enter its familiar area when displaced outside of it, and is also capable of prompt orientation towards the home direction. What are the orientation strategies needed to carry out such behavioural tasks?

For homing purposes a given species can resort to two different orientation strategies, by using either egocentric (body-centred) or geocentric (world-centred) systems of reference (Papi 1992). For the scincid *Tiliqua rugosa*, Freake (2001) proposed a course-reverse homing strategy, since this lizard can use celestial cues, sensed by a sky polarisation compass (Freake 1999), to determine the direction of the outward journey displacement, and then reverse that direction to orient its homing course. In fact, *T. rugosa* specimens displaced with no access to visual cues performed worse in both initial orientation and homing than those that had access to visual cues (Freake 2001). Therefore, *T. rugosa* might refer to an egocentric system of reference to home.

On the other hand, Jenssen (2002) found that *Anolis cristatellus* is capable of homing even if transported in cloth bags excluding any visual cues. Therefore, Jenssen (2002) proposed for that species a geocentric orientation strategy and in particular a pilotage mechanism as “the most parsimonious explanation for the homing performances of *A. cristatellus*”.

Using pilotage, a lizard may use a non ordered complex of landmarks, generalising between the familiar and the unfamiliar ones. When exposed to a new array of landmarks, a lizard may geocentrically fix its position relative to home, continuing to take into account both its new location and that of the familiar area. This ability corresponds to the acquisition of a topographic or cognitive map without using a compass, which is type five in the classification of homing phenomena proposed by Papi (1990).

The present results show that YVIS lizards, independently of the distance of release, all headed in a homeward direction with complete success in re-entering their familiar area. This result is shared with the NVIS lizards, that performed better than the YVIS in one case (A Series). Furthermore, lizards were transported to the release spot along some existing footpaths with abrupt angular change in the course of outward journey. All this supports the use by *P. siculus* of an allocentric pilotage strategy to re-enter home from the release spot, as proposed by Jenssen (2002) for *A. cristatellus*. This strategy is perhaps shared with *P. muralis* (Scali et al. 2013) and other

species of lizards that were displaced with no access to visual information during the outward journey (e.g. Ellis-Quinn & Simon 1989, 1991).

Alternatively *P. siculus* may use a mosaic map (sensu Wallraff 1974), also called by Baker (1978) a “familiar area map”. This mosaic map is formed by the learned spatial relationships between a system of local cues used to calculate the home direction. These relationships can be learned as compass directions, while the range of exploration determines the extent of the map (Wiltschko & Wiltschko 1982; Wallraff et al. 1994).

P. siculus, as well as other species of lizards, have a time-compensated sun compass (Foà et al. 2009; Beltrami et al. 2010) to determine spatial directions. The fact that all displaced lizards came back to their familiar areas, irrespective of the distances at which they were released, suggests that *P. siculus* may actually use a mosaic map, i.e. a navigation system more efficient than pilotage.

Future investigations still need to establish whether *P. siculus* effectively use a mosaic map-based homing strategy, with an enlargement of the dislocation range in different complexity of habitat, and without a direct view of the familiar areas. That should be the future goal in the field of the navigation capabilities of lizards.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

ETHICAL STANDARD

All protocols performed in the study involving animals comply with the ethical standards and Italian laws on animal welfare.

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