Homing behavior of a tree lizard: influences of mating resource and habitat structure

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Handling Editor: Quinn Webber

Homing behavior, characterized by repeated navigation to specific spatial areas, is shaped by individual condition and numerous environmental factors varying at both individual and population levels. Homing behavior is often measured by quantifying site fidelity and homing success. Site fidelity reflects an individual's inclination to stay or reuse its previously occupied location, while homing success assesses the likelihood of an individual returning to its original location after an involuntary translocation. Exploring the effects of ecological and environmental factors on homing behavior across populations offers valuable insights into its adaptability to diverse and changing environments. Here, we conducted a translocation experiment involving 8 populations of Swinhoe's tree lizard (*Diploderma swinhonis*). We examined the effects of resource availability (mate and food), morphological traits, habitat structure, and population density on both site fidelity and homing success. Our results revealed significant variations in both site fidelity and homing success, both within and between populations. Males exhibited higher site fidelity when they had high numbers of female neighbors and low levels of heterogeneity of male neighbors. Regarding homing success, males returned to their territories more rapidly when their territories provided abundant mating opportunities and low levels of intrasexual competition. Additionally, habitat structure influenced homing success, with males showing higher success rates in populations characterized by smaller trees, or when they occupied smaller territory trees. Overall, our findings emphasize the necessity of making comparisons within and between populations to better understand the evolutionary and ecological forces shaping animal navigation.

Key words: cross-population variation; homing success; site fidelity; the Swinhoe's tree lizard (*Diploderma swinhonis*).

Introduction

Movement through the environment is a fundamental animal behavior shaped by spatiotemporal variation in resources (Willems and Hill 2009; Willems et al. 2009). Animal movement has profound effects on both evolutionary fitness and ecological processes, depending on the behavioral context and travel distance involved (e.g. migration, dispersal, foraging, and mate searching, Hooten et al. 2017; Lewis et al. 2021). To thrive in a fluctuating environment, animals must efficiently locate distributed resources (e.g. food, mates, and shelter) in order to gain access to them (Williams and Safi 2021). This process necessitates integrating information obtained from the environment with locomotory behaviors (Åkesson et al. 2014; Breed and Moore 2016). Advancing our understanding of movement not only illuminates the complexities of animal sensory systems and cognition (Fagan et al. 2013; Lewis et al. 2021), but also informs the development of conservation plans for endangered species (Allen and Singh 2016; Hromada et al. 2023).

Animals often reuse specific objects or locations within their environment, such as shelters, nests, and territories. Relocating these sites across space and time involves homing (Gerking 1959; Papi 1992; Breed and Moore 2016). Homing in animals is typically defined as navigation back to a specific location through unfamiliar areas, setting it apart from long-distance movements like dispersal and migration (Humphries and Sisson 2012; Breed and Moore 2016; Galib et al. 2022). To navigate home, animals employ various sensory cues and use several types of sensory information and cognition, such as landmark piloting, path integration, and cognitive maps. (Papi 1992; Pašukonis et al. 2014a; Breed and Moore 2016). For example, pigeons rely on solar and geomagnetic cues for homing (Grüter and Wiltschko 1990; Armstrong et al. 2013), whereas lizards are known to primarily use sun compass information and visual cues to orient and navigate home (Zuri and Bull 2000; Freake 2001; Foà et al. 2009; LaDage et al. 2012; Gagliardo 2013). While the "how" of sensory and cognitive mechanisms

facilitating animal homing behavior has been extensively discussed, further investigation is needed to develop a more complete understanding of the "why"—the role that assessing the costs and benefits of homing plays in variation of homing outcomes in an ecological context.

Two criteria, site fidelity and homing success, are generally used to characterize the homing behavior of a species (Jreidini and Green 2022). Site fidelity is defined as an individual's inclination to stay or reuse its previously occupied location, strongly connected with the tendency of homing (Switzer 1993; Jiménez-Franco et al. 2013; Richardson et al. 2017). Homing success, on the other hand, is experimentally characterized as the likelihood that an animal returns to its original location following an involuntary translocation to an unfamiliar site (Grüter and Wiltschko 1990; Papi 1992). Both site fidelity and homing success can be influenced by a combination of individual intrinsic conditions and environmental factors. Individuals are expected to tend to return home (i.e. evolve increased homing tendency) when the benefit of homing outweighs the cost (Ellis-Quinn and Simon 1989). For instance, site fidelity and homing success increase with mating resources, as these directly influence reproductive fitness (Hoover 2003; Bai and Severinghaus 2012; Navarro-Salcedo et al. 2022). Additionally, larger individuals, often older and more experienced, may have better understanding of their local environment, aiding them in finding their way home (Weintraub 1970; Ellis-Quinn and Simon 1989). Their size advantage also helps them repel intruders, ultimately enhancing site fidelity and homing success (McEvoy et al. 2013).

Studies investigating interpopulational variation in homing behavior are valuable for providing deeper insights not only into how environmental heterogeneity shapes homing behavior, but also into how animals navigate under diverse environmental conditions. For example, although Scali et al. (2012) found that homing behavior varied within a species of wall lizards (*Podarcis muralis*), the mechanisms causing this variation were not well elucidated. Homing behavior is likely shaped by a variety of factors that differ between populations (e.g. resource distribution, habitat structure, population density). For instance, in White's

skinks (*Liopholis whitii*), significantly smaller home ranges were observed when high-quality sites were distributed uniformly (Halliwell et al. 2017), implying that skinks move more in response to uneven resource distribution. Hence, resource distribution would also be expected to change homing tendency and thus affect the outcome of homing experiments. As another example, an environment with denser vegetation and more abundant vertical obstructions could hinder animal locomotory performance (Losos and Irschick 1996; Neel et al. 2021) and restrict their ability to use visual landmarks to navigate (Papi 1992; Janson and Bitetti 1997; Freake 2001; Auburn et al. 2009). This suggests that habitat structure and complexity should also have a major impact on homing outcomes (Bélisle et al. 2001). Additionally, population density and resource distribution would also be expected to affect the overall magnitude of social interaction among individuals (Fletcher Jr 2007) and the level of resource competition (Harada et al. 1995), thereby altering the potential benefits of homing. However, empirical studies are needed to investigate these factors, as expectations regarding variation in homing can be contradictory: individuals from populations with more abundant resources could exhibit a higher degree of site fidelity because of their desire to retain and defend a high-resource territory (Carpenter 1984; Hoover 2003; Wasko and Sasa 2012; Cram et al. 2013), but they may also exhibit a lower homing tendency after translocation because resources remain abundant at their new location (Rueger et al. 2016). The 2 mutually inclusive arguments once again emphasize the need for homing studies that compare outcomes across multiple populations.

Here, we aimed to investigate how site fidelity and homing success vary within and between populations of a territorial terrestrial vertebrate by using the Swinhoe's tree lizard (*Diploderma swinhonis*) as a model system (Fig. 1). Swinhoe's tree lizard is the largest endemic tree lizard species in Taiwan, inhabiting diverse environments from natural forest to urban parks. These lizards exhibit strong sexual dimorphism, with males significantly larger than females and featuring a distinctive yellow lateral stripe (Kuo et al. 2009; Norval et al. 2011). Adult male Swinhoe's tree lizards are highly territorial, often occupying a single tree—referred to
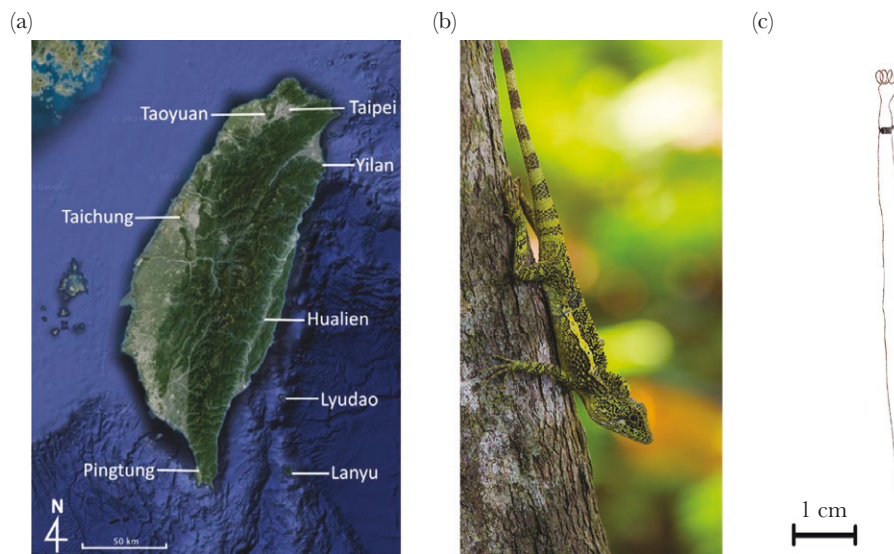

Fig. 1. The study system for our homing experiment. a) A map of the 8 sample populations ranging from urban parks to natural forests across Taiwan. The satellite photo is extracted from Google map (Imagery ©2024 TerraMetrics, Map data ©2024). b) An adult male Swinhoe's tree lizard, the largest agamid in Taiwan, in typical territorial display posture. c) The harmonic radar tag, crafted with a silver-jacketed-wire soldered onto a diode, featured an optimized shape enabling detection from 20 to 30 m using a RECCO R9 detector.

as the territory tree—for resting, basking, and territorial displays. When an intruder enters their territory, males perform pushups and dewlap displays to drive the intruder away (Hsu et al. 2023). Males rarely overlap their territories or share the same territory tree (Lin and Lu 1982). In contrast, 2 or 3 females are often observed at the same tree, and most female home ranges overlap with those of males, suggesting that the mating system is polygynous (Lin and Lu 1982). In tree-dwelling lizards, the degree of polygyny often increases with tree size (Manzur and Fuentes 1979; Cuadrado 2001). Previous studies found that dominant male Swinhoe's treel lizards perch higher and use thicker trunks and branches than non-dominant males and females, suggesting that territory tree size and perch height are potential factors influencing the level of polygyny and territory dominance (Lin and Lu 1982; Kuo et al. 2007, 2009).

Thus, Swinhoe's tree lizard represents an ideal study system for studying homing behavior for several reasons. First, the territoriality of males makes it relatively easy to delineate territorial boundaries. Second, the species is a habitat generalist, affording us the advantage of exploring variation across populations that differ in key environmental parameters. Third, our previous study has revealed a negative density-dependent territoriality in this species (Hsu et al. 2023), indicating that behavioral differences evolve readily among different populations. To address our research questions, we conducted a translocation experiment, designed to examine the effects of morphological traits, resource availability, habitat structure, and population density on homing behavior.

Materials and methods

Study system

The experiments were conducted during the breeding season (June–October) of 2022, using 8 populations of the Swinhoe's tree lizard in Taiwan. The study locations included Taipei (N25.017702°, E121.553213°), Taoyuan (N25.002531°, E121.328678°), Taichung (N24.146324°, E120.557401°), Pingtung (N22.158263°, E120.709238°), Yilan (N24.614233°, E121.853024°), and Hualian (N23.619645°, E121.419735°) on the mainland, as well as 2 offshore islands, Lyudao (N22.656645°, E121.487146°) and Lanyu (N22.027989°, E121.577290°) (Fig. 1). The study populations comprised natural broadleaf forests in Taipei, Lyudao, and Lanyu, each interspersed with hiking trails. In contrast, Taoyuan, Taichung, Pingtung, and Hualien featured artificial forests (urban parks maintained by humans for recreation) with intersecting pathways. Additionally, Yilan was a forested area within an elementary school, located next to the playground.

The distinctive behavior of occupying a single tree and maintaining territoriality guided our delineation of territory boundaries. Lin and Lu (1982) found that the average territory size of adult male lizards is 33.45 ± 14.9 m², ranging from 6.18 to 77.1 m², approximately equivalent to a circle with a diameter of 2.5 to 5 m. Additionally, during our pretest observations, we found that 76% of relocations were located within 6 m of the territory tree (Supplementary Table S1a). After averaging for each male, 78% of the males were present within 6 m of the territory tree (Supplementary Table S1b). Additionally, we noted that males were rarely seen on their original territory tree once the distance between the lizard and the tree exceeded 6 m. As a result, we defined the territory as a circle with a radius of 6 m, centered on the territory tree. Thus, a lizard was considered to be remaining on or returning to its territory if it was within 6 m of its original territory tree.

Experimental preparation

Fieldwork for measuring site fidelity and homing success was conducted daily from 9:00 to 12:00 and 13:30 to 16:30 in the breeding season of 2022. We captured a total of 320 male lizards with hand lassoes (40 male territory owners at each population). To ensure that each captured male was indeed a resident, we limited our capture to males that exhibited pushup behavior on their territory tree because males rarely did pushup behavior when they were outside their territories during our pretest observations. The tree that each lizard was observed to use for perching, displaying, and central-place foraging was considered its territory tree and we marked individual territory trees with numbered tags. Additionally, because territory tree size and perch height can be associated with an individual's dominance level, we also measured the perching height of each male before capture, along with the size of an individual's territory tree by measuring its diameter at breast height (DBH). Also, because larger lizards tend to be more dominant males that win fights more often and are more capable of defending or reoccupying territories, we also measured lizard body weight to the nearest 0.1 g using an electronic balance, and snout-vent length (SVL), head length (HL), head width (HW), and head height (HH) to the nearest 0.1 mm using digital calipers.

To track the location of lizards during the experiment, each captured lizard was marked with paint corresponding to the color and number as its tree tag (our previous study indicated that tag color does not affect conspecific interactions; Hsu et al. 2023). We also attached a harmonic radar tag (RECCO avalanche rescue system, Lidingö, Sweden), a small radio reflector for tracking small animals (O'Neal et al. 2004; Brazee et al. 2005), to the dorsal side of each lizard using breathable tape. Each tag was an antenna made of a silver-jacketed-wire (15 cm long before making a loop and coils, 0.5 mm diameter, UL1423) soldered to a diode (Fig. 1). On 1 side of the tag, the wire was looped and consisted of 5 coils [2 mm diameter to enhance the signal (Brazee et al. 2005)] with a diode bridging the gap of the loop. The other side of the tag was a 1.9 cm unbent wire. Each tag weighed 0.005 g [i.e. much less than 5% of lizard weight (Wilson and McMahon 2006)] and could be detected from 20 to 30 m away using the RECCO R9 receiver.

Site fidelity and homing experiments

To test site fidelity, 10 lizards from each population were released back to their territory trees after processing. To test homing success, the other 30 lizards from each population were randomly assigned to one of the distance treatments (i.e. 20, 40, and 60 m, $N = 10$ each treatment) and translocated after processing. To reduce observer bias, a pre-assigned treatment order was determined prior to capture and the 40 lizards from each population were assigned chronologically to treatments. The direction of the translocation site was determined randomly (by throwing a pen, with the direction indicated by the pen's pointing). If a translocation site was inaccessible (e.g. cliffs, steep slopes, and rivers), the direction was determined again. Prior to release or translocation, lizards were placed in an opaque cloth bag and translocated within 1 min in order to control the effects of handling time and visual-based memory on their homing behavior (Freake 2001). To avoid potential learning effects, each lizard was used only once in the experiment (ten Cate and Rowe 2007).

To assess site fidelity and homing success, we monitored lizards twice a day for 7 consecutive days (14 total observations) after their release or translocation. During each monitoring session, we walked slowly along transects and carefully scanned the

study population using a handheld RECCO R9 detector. When we found a tagged lizard, we recorded the time and location using a handheld Global Positioning System (GPS) device (Garmin Etrex 32x). We also measured the shortest linear distance between the lizard and its original territory tree. If the distance was 6 m or less, the lizard was considered to have stayed within or returned to its territory. Site fidelity was calculated as the number of times a lizard stayed within its territory divided by 14 (the total number of monitoring sessions). For lizards that homed, we also recorded the time it took a tagged lizard to return to its territory. To investigate how male-male competition and potential mating opportunities affect site fidelity and homing success, we recorded the number of untagged males and females (i.e. "neighbors") present in each lizard's territory during each of the 14 monitoring sessions. We then calculated the average number of untagged males and females across these sessions to determine the average number of male neighbor intrusions (male neighbors) and average number of female neighbor intrusions (female neighbors) for each territory.

Population-level parameters

To investigate the effect of population-level factors on site fidelity and homing success, we quantified population density, food abundance, and habitat structure for each population. We estimated population density using data from surveys conducted from 2013 to 2014 (Pingtung, Lyudao, and Lanyu) and 2018 to 2020 (Taipei, Taoyuan, Taichung, Yilan, and Hualien) that used the quadrat method, a widely employed technique for population density assessment (Gleason 1920). Each of the populations was surveyed for 5 d under sunny conditions with temperatures ranging from 30 to 33 °C. A 1,250 m² experimental quadrat was used, and all lizards within the quadrat were captured with hand lassoes. Captured lizards were marked with nontoxic acrylic paint to avoid repeated sampling. After marking, we immediately released lizards back to their capture sites to minimize disturbance. The number of males or females within a quadrat were taken as sex-specific density estimates for each population. Although experiments were not conducted at the same time population densities were estimated, previous studies of this species have found that population density in these locations has remained stable across several decades of monitoring (since 2006) (Hsu et al. 2023; Lin et al. 2023); thus we assumed that the previously measured populations densities are likely to represent realistic estimates of density within the timeframe of the experiments.

We used ground pitfall traps to collect prey samples over a period of 5 d during the breeding season from 2018 to 2021 to assess food abundance at each of the 8 populations. Each population was sampled using 3 sets of traps, consisting of four 0.6 L plastic tubes arranged in a Y shape and buried underground. The tubes were filled with a trapping solution of 30 ml of 75% alcohol. Prey samples collected from the traps were categorized by taxonomic order to quantify food abundance. Because Swinhoe's tree lizards rarely eat individuals smaller than 3 mm, individuals larger than their gape size (approximately 3 × 3 cm²), and large African snails, we excluded these categories of prey from further analyses (Huang 2007; Hsu et al. 2023). We oven-dried prey samples at 40 °C for 3 d to obtain dry mass for each set of traps. The food abundance of each population was calculated as the average dry mass of all sets of traps within each population.

We also characterized the habitat structure of each population concurrent with fieldwork on experimental translocations (spring/summer of 2022). For this purpose, we defined spatial boundaries by extending 10 m outward from both sides of the lizard monitoring transects we used. We then divided this area into multiple 10 × 10 m² quadrats and randomly selected quadrats that represented a total of 30% of the population area. Habitat characteristics within each selected quadrat were measured using a square polyvinyl chloride frame (i.e. 50 × 50 cm²). We threw the frame in 4 different directions (i.e. N, W, S, and E) from the center of each quadrat. We recorded habitat type and number of stems and trunks within the frame, as well as distance to the nearest tree and DBH of the nearest tree from the frame center. To quantify the coverage (%) of each habitat type within the frame, we took a bird's eye view photo using a digital camera (Olympus Tough TG-5, IM005). The frame consisted of 25 grids (i.e. 10 × 10 cm²) and we categorized each grid as a habitat type (i.e. grass, herb, rock, mulch, bare land, manmade construction, and others) if it covered more than 50% of the grid area. The number of grids categorized for a specific habitat type out of the 25 grids represented its coverage.

Statistical analysis

Prior to analysis, we estimated the heterogeneity of resource distribution and average site fidelity for each population, as these were factors that could potentially explain variation in site fidelity and homing success (Switzer 1993). To account for the heterogeneity of resource distribution, we estimated the coefficient of variation for several individual factors, including average male neighbors, average female neighbors, and territory tree size. Higher heterogeneity corresponds to more variable resource distribution, with some territories containing higher levels of resources than others. Also, high heterogeneity in the number of neighbors indicates unevenness of the distribution of individuals. Additionally, to investigate the effect of site fidelity on homing success at the population level, we calculated the average site fidelity for each population by averaging the site fidelities of the individuals within that population.

Before analysis, we conducted several data transformations to avoid potential correlations between factors. First, we estimated the body condition of each sampled lizard by measuring the residual of a simple linear regression fitting log-transformed body weight against log-transformed SVL (Harris 2008). We also averaged the values of each habitat structure collected from multiple frames for each population. Next, we subtracted the values of habitat tree size from the territory tree size according to the population of each lizard to obtain the relative tree size (i.e. a measure of how much bigger or smaller the territory tree was compared to other trees within that population). Finally, we conducted principal component analyses (PCA) to reduce the dimension of a suite of morphological traits (namely, SVL, HL, HW, HH, weight, and body condition), as many of these traits can be highly correlated with each other (Table 1; Supplementary Table S1). We retained the major principal components from the morphology PCA that cumulatively explained > 85% variation for further statistical analyses.

To investigate how site fidelity was affected by factors at both individual and population levels, we ran mixed effect binomial logistic regression models with the "bglmer" function in the "blme" R package version 1.0-5 (Chung et al. 2013). We standardized (i.e. mean = 0 and standard deviation (SD) = 1) all numeric explanatory variables before analyzing and conducted a forward stepwise model selection process, which included 3 steps. In the basic model, we assigned a random intercept among populations and a random intercept among individuals nested within each

Table 1. The potential a) individual-level and b) population-level factors that shape homing behavior. Abbreviations: SVL, snout-vent length; HL, head length; HH, head height; HW, head width; DBH, diameter of breast height; and CV, coefficient of variation.

Explanatory variable	Description
(a) Resource availability	
Average female neighbors	Mean of nonresident (i.e. neighboring) females observed in a territory across monitoring sessions
Average male neighbors	Mean of nonresident (i.e. neighboring) males observed in a territory across monitoring sessions
Morphological traits	
PC1	Longer SVL, HL, and HH and heavier weight
PC2	Greater body condition
PC3	Longer HW
Habitat structure	
Territory tree size	DBH of the territory tree
Perch height	Height where each male located on the territory tree
Treatment	
Displacement distance	Distance from the territory tree to the translocation site
(b) Resource availability	
Heterogeneity of female neighbors	CV of average female neighbors
Heterogeneity of male neighbors	CV of average male neighbors
Food abundance	Mean weight of prey samples caught in pitfall traps
Population density	
Male density	Number of males within 1250 m^2
Female density	Number of females within 1250 m^2
Habitat structures	
Habitat tree size	Mean DBH of trees nearest to survey points
Heterogeneity of territory tree size	CV of territory tree size
Distance to the nearest tree	The distance between the frame and its nearest tree
Number of stems	Average number of stems within the 1-meter-radius circle centering the frame of each population
Number of trunks	Average number of trunks within the frame of each population
Coverage of grass	Average coverage of grass of each population
Coverage of herb	Average coverage of herb of each population
Coverage of rock	Average coverage of rock of each population
Coverage of mulch	Average coverage of mulch of each population
Coverage of bare land	Average coverage of bare land of each population
Coverage of manmade construction	Average coverage of manmade construction of each population
Site fidelity	
Average site fidelity	Mean site fidelity of each population

population to accord with our experimental design, which involved sampling 8 populations and repeatedly monitoring ten lizards nested from each population. These 2 random intercepts allow us to cope with pseudoreplication of populations and individuals due to repeated measurements. In the first step, to control intrapopulation effects that previous homing studies highlighted, we focused on individual-based fixed factors. These included average male neighbors, average female neighbors, PCA-derived morphological traits (PC1, PC2, and PC3), territory tree size, and perch height (Table 1). Using a forward stepwise approach, we included the factor that resulted in the greatest decrease of the Akaike information criterion (AIC) value in each step until no further reduction was observed. Once 2 factors were included in the model, their interaction was also considered as a candidate. In the second step, to examine the additional interpopulation effects, we focused on population-based factors. These candidate factors included male density, female density, heterogeneity of male neighbors, heterogeneity of female neighbors, food abun-

dance, habitat average tree size, heterogeneity of territory tree size, distance to the nearest tree, number of stems, number of trunks, and coverage of habitat components (grass, herb, rock, mulch, bare land, and manmade construction). Following the same forward stepwise process, we included the factor that most decreased the AIC value at each step until no further reduction was observed. Interactions between each of the 2 included factors were also considered as candidates. In the third step, we examined the random slope of included individual-based covariates varying within population to investigate whether the intrapopulation effect of these covariates varied among populations. If including the random slope decreased the AIC value, it was retained in the model.

To investigate how homing success was affected by factors at both individual and population level, we ran mixed effect Cox proportional hazards model with the function "coxme" in the R package "coxme" version 2.2-20(Therneau 2024). As with the model selection procedure we used for site fidelity, we first

standardized all explanatory variables and then conducted a 3-step model selection procedure. In the basic model, we assigned the random intercept of population and the distance treatment (i.e. 20, 40, and 60 m). In the first step, to examine the intrapopulation effect, we focused on individual-based fixed factors. These included average female neighbors, average male neighbors, PCA-derived morphological traits (PC1, PC2, and PC3), territory tree size, and perch height (Table 1). We conducted a forward stepwise procedure which included the factor which resulted in the greatest reduction of the AIC value at each step until no further reduction was observed. Once 2 factors were included, their interaction was also considered as a candidate. In the second step we focused on the population-based factors. These included male and female population density, heterogeneity of male and female neighbors, food abundance, habitat tree size, heterogeneity of territory tree size, distance to the nearest tree, number of stems, number of trunks, coverage of habitat components (grass, herb, rock, mulch, bare land, and manmade construction), and average site fidelity. Using the same forward stepwise procedure, we included the factor that most decreased the AIC value at each step. Interactions between included factors were also considered as candidates. In the third step, we examined the random slope of included individual-based covariates varying within populations to investigate whether the intrapopulation effect of these covariates varied among populations. If including the random slope decreased the AIC value, it was retained in the model.

All analysis was conducted using R (R Core Team 2024) using an alpha level of 0.05 to determine statistical significance.

Ethics statement

Permission to collect and observe the lizards was issued by the institutional animal care and use committee of National Museum of National Science (NMNSAAAUP2019-001).

Results

PCA of morphological traits

The PCA of morphological traits explained 95% of the variation in trait data, with the first 3 components (PC1–3) explaining 53%, 21%, and 21% of the variation, respectively (Supplementary Table S1). The first axis (PC1) largely corresponded to individual size, as the main contributions were SVL, HL, HH, and body weight. The second axis (PC2) largely represented body condition, and the third axis (PC3) was mainly associated with HW (Table 2).

Site fidelity

Male site fidelity varied across the 8 populations of Swinhoe's tree lizard, but overall males were found on their territory during 54.17% of surveys. Four individual-based factors/interactions decreased the best-fit AIC by 3.77, and then 2 population-based factors resulted in an additional decrease of 6.27, indicating that the population-based factors were strong predictors of site fidelity (Supplementary Table S2).

Among the individual-based factors, we found that males remained in their territories more often when more female neighbors were in their territories (odds ratio, OR = 1.438 per SD, $Z = 1.980$, $P = 0.048$; Fig. 2a; Supplementary Table S3). In addition, perch height was positively associated with site fidelity (OR = 1.362 per SD, $Z = 1.921$, $P = 0.055$; Supplementary Table S3). However, these factors did not serve as strong predictors of the variation of site fidelity across populations, as the effects of random slopes of average number of female neighbors and perch height were excluded from our model. We did not find a significant effect of either the average number of male neighbors ($P = 0.766$) or the interaction between perch height and average number of male neighbors ($P = 0.109$). PCA-derived morphological traits, and territory tree size were not represented in the best model (Supplementary Table S3), implying no significant effects of these individual-based factors on site fidelity.

Among the population-level factors, we found that lizards showed a higher degree of site fidelity when the heterogeneity of male neighbors was lower (OR = 0.617 per SD, $Z = -2.443$, $P = 0.015$; Fig. 2b; Supplementary Table S3) within a population. In addition, coverage of rock of each population was negatively associated with site fidelity (OR = 0.697 per SD, $Z = -1.806$, $P = 0.071$; Supplementary Table S3). Population density, the heterogeneity of female neighbors, food abundance, habitat tree size, the heterogeneity of territory tree size, distance to the nearest tree, number of stems or trunks, and coverage of other habitat components did not show a significant association with site fidelity as they were not included in the top model (Supplementary Table S3).

Homing success

Homing success varied across populations, with 167 of 240 (69.5%) individuals successfully returning home. Males translocated shorter distances were more likely to home: 68 of 80 (85.0%) males displaced 20 m homed with an average of 1.441 ± 1.300 d to return to their territory tree; 57 of 80 (74.0%) males displaced 40 m homed within 1.737 ± 1.433 d; and 39 of 80 (48.8%) males displaced 60 m homed within 1.949 ± 1.445 d. Our model selection procedure resulted in 3 individual-level factors decreasing AIC by
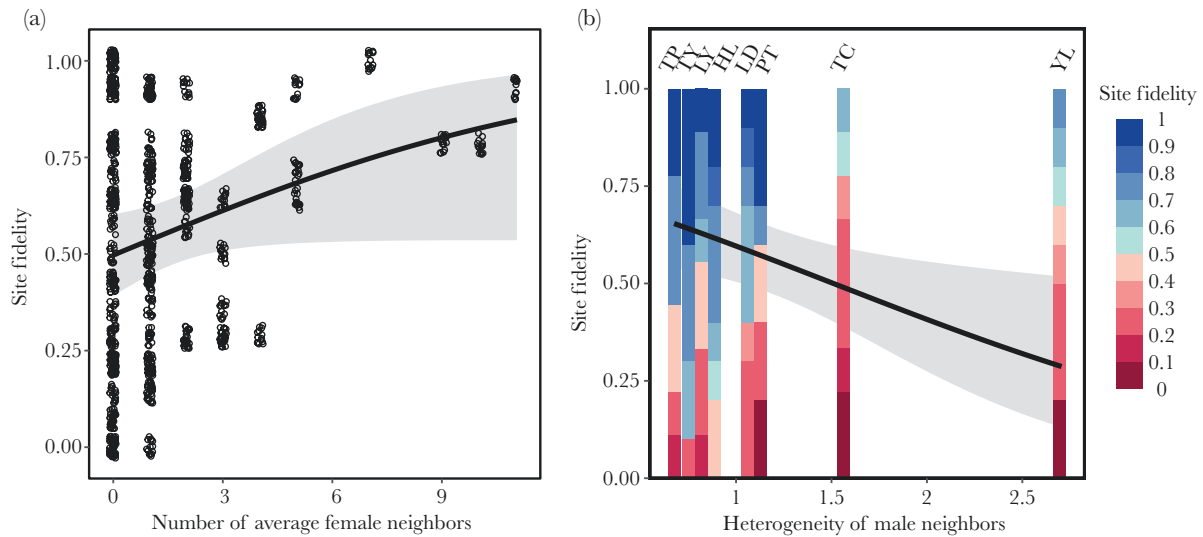
Table 2. Summary of PCA loadings and proportion of variation explained by downscaling morphological variables among 8 locations.

Variable	Component		
	PC1	PC2	PC3
SVL	0.93	−0.10	0.27
HL	0.82	0.05	0.46
HW	0.44	0.12	0.89
HH	0.86	0.20	0.30
Weight	0.84	0.43	0.26
Body condition	0.08	0.99	0.08
Proportion variance	0.53	0.21	0.21
Cumulative variance	0.53	0.74	0.95

Fig. 2. The conditional effects of a) number of average female neighbors in the territory and b) the heterogeneity of male neighbors on site fidelity. The solid black line and the gray area indicate the average effect of each factor and its 95% confidence band, respectively. In figure (b), each bar represents a population, with the colors indicating the proportion of the level of site fidelity. Abbreviation: TP, Taipei; TY, Taoyuan; TC, Taichung; PT, Pingtung; YL, Yilan; HL, Hualien; LD, Lyudao; LY, Lanyu.
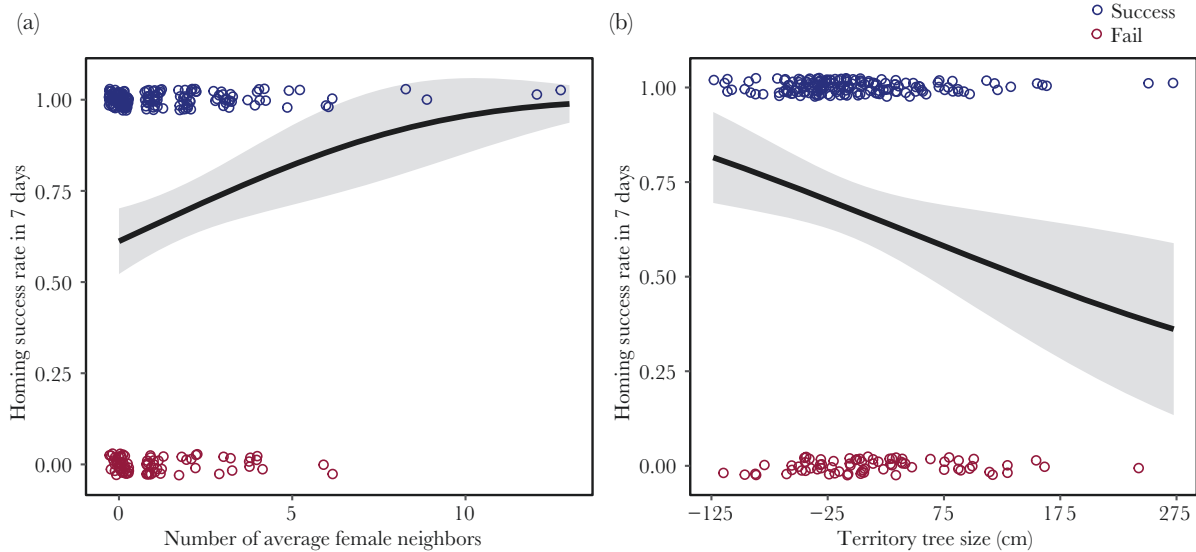

Fig. 3. The conditional effect of a) number of female neighbors in the territory (i.e. mating opportunity) and b) territory tree size on homing success. The solid black lines and the gray areas indicate the average effect and their confidence bands. The blue circles present successful homing events, and the red circles represent failed homing events.

4.31, and then 5 population-level factors/interactions decreasing AIC by 8.86, indicating that, as with site fidelity, population-level factors were strong predictors of male homing success (Supplementary Table S4).

For individual-level factors, we found that male lizards were more likely to return to their territories when translocation distance was shorter (Hazard ratio, HR = 0.614 per 20 m, Z = − 5.92, P < 0.001; Supplementary Table S5), when there were more female neighbors present in their territories (HR = 1.257 per SD, Z = 2.71, P = 0.007; Fig. 3a), and when their territory tree was smaller (HR = 0.808 per SD, Z = − 2.37, P = 0.018; Fig. 3b). However, although the average number of female neighbors and tree size showed a strong effect on homing success at an individual level, they were not strong predictors of the

variation in homing success across populations, as the effects of the random slopes of these factors were excluded from our model. PCA-derived morphological traits and perch height were also not included in the top model (Supplementary Table S5).

Among the population-level factors, the average number of male neighbors, female density, and their interaction affected lizard homing success (Female density: HR = 1.155 per SD, Z = 1.52, P = 0.130; average male neighbor: HR = 0.676 per SD, Z = − 2.88, P = 0.004; female density × average male neighbor: HR = 0.955 per SD, Z = 2.52, P = 0.012; Supplementary Table S5). Males from populations with higher female densities were more likely to return to their territory regardless of male neighbors, whereas those from populations with lower female densities tended not to return to
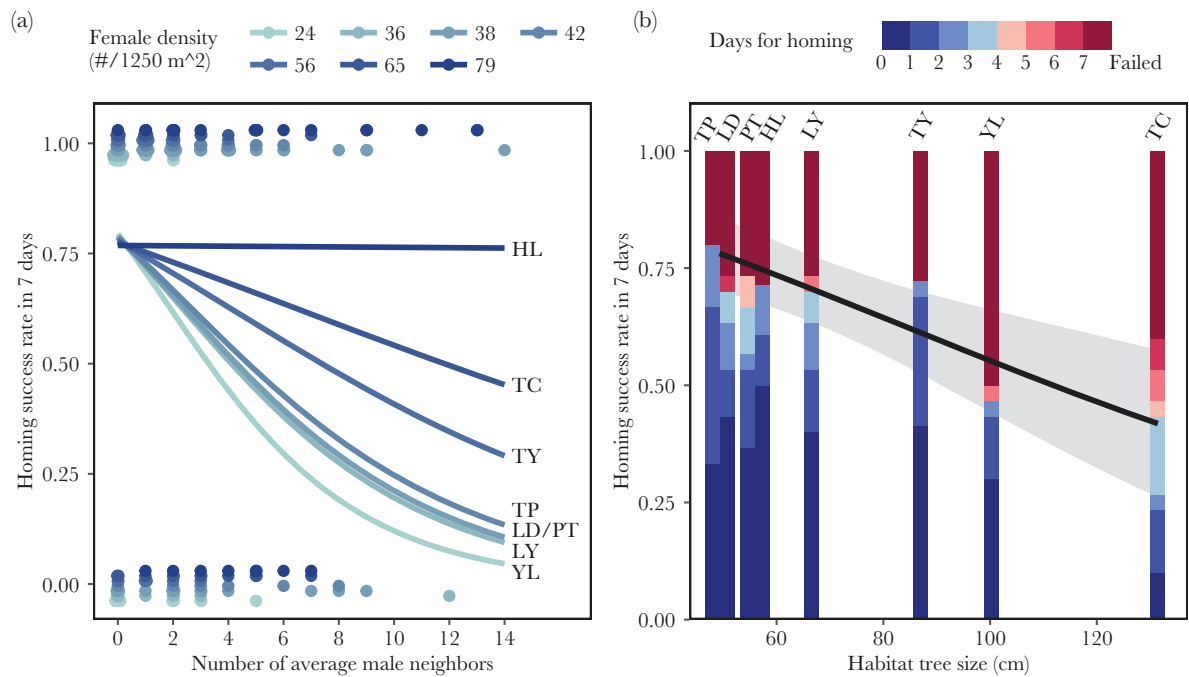
Fig. 4. The conditional effect of a) the interaction between female population density and number of male neighbors (i.e. male-male competition pressure) and b) habitat tree size on homing success. In figure (a), the solid lines present the average effect. The color of the lines and circles indicate female density for each population. The circles located at 1.00 denote successful homing, whereas those at 0.00 denote failed homing attempts. In figure (b), the solid black line and the gray area present the average effect and the confidence band. Each bar represents a population, with the colors indicating the proportion of days spent in homing. Abbreviation: TP, Taipei; TY, Taoyuan; TC, Taichung; PT, Pingtung; YL, Yilan; HL, Hualien; LD, Lyudao; and LY, Lanyu.

their territories when they had a large number of male neighbors (Fig. 4a). We also found that homing success of lizards increased in populations with smaller trees (HR = 0.706 per SD, Z = − 3.42, P < 0.001; Fig. 4b; Supplementary Table S5). The interaction between average male neighbors and habitat tree size showed no significant effect on homing success (P = 0.140). The heterogeneity of female number, the heterogeneity of male number, male density, food abundance, the heterogeneity of territory tree size, distance to the nearest tree, number of stems or trunks, coverage of habitat components, and mean site fidelity of each population were all dropped from the top model (Supplementary Table S5).

Discussion

Our study demonstrates empirically that site fidelity and homing success of individuals can vary significantly both within and between populations. We examined the impact of multiple ecological and environmental factors on the homing behavior of male Swinhoe's tree lizards across 8 populations and identified several factors that strongly affected homing behavior—most of these were related to the availability of ecological resources. These findings are an important contribution because the literature on animal homing is dominated by studies addressing the mechanisms of homing ("how" animals navigate unfamiliar terrain to go home—e.g. Freake 2001; Hansson and Åkesson 2014; Pašukonis et al. 2014a, 2014b; Breed and Moore 2016; Mandal 2018). Additionally, previous studies on the adaptive function of homing ("why" animals return home) mostly focus on individual variation in this behavior (Freake 1998; Scali et al. 2012; Streit and Bellwood 2017; Nothacker et al. 2018). Our study is unique in that it not only explores the effects of multiple ecological and environmental factors on site fidelity and homing success, but we also incorporated factors that vary at both the individual and popula-

tion levels, giving us novel insights into the factors that shape the evolution of homing behavior.

With respect to site fidelity, male lizards exhibited higher site fidelity when there were more female neighbors present within their territories. As more female neighbors may indicate more abundant mating opportunities, this finding suggests that the reproductive benefits provided by a high-quality territory could motivate high levels of site fidelity (Navarro-Salcedo et al. 2022; Rebstock et al. 2022). At the population level, we found that males had higher site fidelity when number of neighbor males was more homogenous within a population (i.e. a more uniform distribution of competitors). Because Swinhoe's lizards are highly territorial, a more uniform distribution is likely when either resources are evenly distributed, and/or individuals have reached an equilibrium between gaining more resources and engaging in more territorial conflict. In either case, a male leaving its territory would incur high costs, as its territory could readily be taken over by other males and it would need to fight for a new territory that still contained a similar level of resources.

Similarly, our analysis of homing success showed that homing behavior likely reflects individuals balancing out the cost and benefit of returning home (Ellis-Quinn and Simon 1989). We found that, overall, the likelihood of a male returning to its territory was highly affected by mating opportunity, intrasexual competition, and habitat structure. More specifically, we found a clear trend indicating that males are more likely to return to a territory that had relatively more female and fewer male neighbors. Furthermore, the significant interaction between the number of male neighbors and female population density indicates that males are more likely to home when their territories have large numbers of neighboring females, regardless of the number of male competitors. This more nuanced understanding illustrates how homing decisions reflect both the potential

reproductive benefits and costs of intrasexual competition a male has experienced within its territory. This also highlights the benefit of examining multiple potential factors simultaneously across populations, as these factors could not be quantified in the study of a single population.

Our findings also suggest that habitat structure could moderate species homing success, potentially by influencing visual landmarks. We found that males were more likely to home successfully when they came from a population containing relatively small trees (a population-level factor), or when their territories were on relatively small trees (an individual-level factor). We can think of 2 plausible explanations for these patterns. First, the reason that males living in populations with larger trees home poorly could simply be because large trees provide more visual obstruction, making visual navigation more challenging. Furthermore, the association between individual territory tree size and homing success could be a byproduct of tree size structure across populations, as males are more likely to reside on large-tree territories in populations with larger average tree size. Second, another potential explanation for our observation that males occupying a large-tree territory exhibited poorer homing success could be that these dominant males did not need to return to their original territories, as they could readily establish a territory in a new site after translocation. Being able to defend a large-tree territory could be a reflection of resource holding power, or male dominance, as suggested by many studies (Manzur and Fuentes 1979; Lin and Lu 1982). Manzur and Fuentes (1979) found that males of tree-dwelling lizard *Liolaemus tenuis* that occupied large trees were bigger and more aggressive, and successfully excluded other males from sites containing multiple females. However, our morphological analyses do not offer support for this line of reasoning. If male dominance affected homing success, then larger-bodied males would be predicted to home less often, but we did not find any influence of morphology on homing success. Overall, the effects of habitat structure on homing suggest that homing success is shaped more strongly by homing ability, rather than homing tendency.

Site fidelity and homing success are often used to assess homing behavior, and homing success results from individuals positively expressing both homing ability and homing tendency (Jreidini and Green 2022). Site fidelity and homing tendency can both be strongly influenced by how an individual evaluates the costs and benefits of defending its territory (Ellis-Quinn and Simon 1989), and are thus likely driven by a similar set of ecological and evolutionary forces. A recent study of Swinhoe's tree lizard (Hsu et al. 2023) found that male lizards were less territorial and expressed weaker bite force when they came from high-density populations. Accordingly, we originally predicted that males from higher-density populations would be subject to high territory turnover, and thus would also show weaker site fidelity and homing tendency. Surprisingly, we did not find any evidence indicating that either male morphology or male population density affecting homing or site fidelity.

Our study indicates that site fidelity and the tendency to home are likely to be shaped by a variety of ecological and evolutionary forces independently. For example, we showed that both the size of individual territory trees and average tree size in a population had a strong negative association with homing success, but the 2 factors did not affect site fidelity. Also, we did not find a significant effect of average site fidelity within a population on individual homing success, as this factor was precluded from the model at the beginning stage of model selection. The non-significant effect of average site fidelity on homing success suggests that

homing ability may play a larger role than homing tendency in determining homing success. However, our study did not examine the potential association between site fidelity and homing success within individuals. Examining this association would require future studies to collect data on both site fidelity and homing success independently from each individual in a population.

In conclusion, our study demonstrates that homing tendencies and abilities are influenced by a complex interplay of mating resources, intrasexual competition, environmental factors, and habitat structure, and thus can vary significantly within and between populations. Our findings underscore the necessity of understanding not only the capabilities animals have evolved to navigate home, but also the motivation they have to do so. This comprehension is essential for understanding variation in animal movement phenotypes within and between populations, as this understanding has numerous implications for the evolution of more long-distance movements associated with migration and dispersal. We anticipate that future research will explore how homing mechanisms adapt under varying natural selection pressures, bridging the "how" and "why" of homing across diverse species.

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

Author contributions

Yu-De Zhang (Data curation [equal], Formal analysis [equal], Writing—original draft [equal]), and Chun-Chia Chou (Conceptualization [equal], Methodology [equal], Validation [equal])

Conflicts of interest

None declared.

Data availability

Analyses reported in this article can be reproduced using the data provided by Zhang et al. 2024.

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