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Movement and Space Use Patterns of the Beale's Eyed Turtle (*Sacalia bealei*) Suggest Sensitivity to Environmental Changes and Poaching

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ABSTRACT

Widespread declines of Asian freshwater turtles demand urgent conservation action. This study used radiotelemetry to track 25 individuals of the Endangered Beale's eyed turtles (*Sacalia bealei*) (12 females, eight juveniles, and five males) in Hong Kong for an average of 284 days. Movement (4.7 ± 8.9 m day^{-1}) and home range (7986 ± 9701 m^2) varied significantly across reproductive class and season, with males exhibiting greater displacement distances and home ranges than females in the wet and mating seasons. *S. bealei* exhibits strong aquatic dependence, favoring deep pools interspaced among riffle-pool sequences. Microhabitat selection varied diurnally and seasonally, with preferences for spatial elements that likely confer concealment advantages. The species' relatively large home range and aquatic dependence highlight its sensitivity to habitat loss and poaching, stressing the urgency for immediate protection of remnant populations. Conservation efforts must prioritize critical stream habitats and leverage telemetry data for informed action.

1 | Introduction

Human activities are driving the global decline of wildlife populations and accelerating rates of species extinction (Pimm et al. 2014; Cox et al. 2022). Freshwater turtles and tortoises are among the most imperiled vertebrates, with over half of the species threatened with a conservation status as Critically Endangered, Endangered, or Vulnerable (Rhodin et al. 2018; Stanford et al. 2020). The main drivers implicated in their declines are overexploitation and habitat loss, though disease and climate change also pose key threats (Stanford et al. 2020). Asian turtles are most impacted, with over 80% of the species threatened and many populations being decimated at alarming rates (Rhodin et al. 2018). This decline is primarily driven by the unsustainable harvest for wildlife trade, which has intensified in recent decades (Cheung and Dudgeon 2006; Sung and Fong 2018).

Animal movement and space use are key to many ecological processes (Nathan et al. 2008; Morales et al. 2010). For instance, the spatial extent may influence resource acquisition and reproductive success (Fontaine and Martin 2006; Mitchell and Powell 2007), while movement patterns may alter species interactions, social organization, and disease transmission dynamics (Morales et al. 2010; Albery et al. 2021). Understanding the movement and space use of turtles is therefore critical to their conservation (Fraser et al. 2018). However, due to the rarity of many Asian turtle species, their movement and space use patterns remain poorly understood.

Endemic to southern China, including Hong Kong, the Beale's eyed turtle (*Sacalia bealei*) is one of the most secretive and poorly known freshwater turtles in the region. Similar to other Asian freshwater turtles, *S. bealei* is heavily poached and its

Summary

Practitioner Points

- Combat poaching by targeted habitat protection. Focus patrols and anti-poaching efforts in stream habitats, particularly around step-pool systems, critical for the survival of *Sacalia bealei*.
- Recognize the importance of concealments. Prioritizing the maintenance or restoration of riparian vegetation and structural complexity in microhabitats to support hiding behaviors is essential in conservation planning for *Sacalia bealei*.
- Increasing the input of telemetric studies on endangered species with remnant populations in Asia is of paramount importance for informing species-specific conservation.

populations are in sharp decline (Gong et al. 2017). In Hong Kong, the species has a scattered distribution, with only a few remaining populations left after decades of poaching (Or and Chan 2025). Consequently, ecological information for the species remains limited (but see Hu et al. 2016; Lin et al. 2018; Sung et al. 2021; Yuan et al. 2025).

Recent studies have investigated various aspects of the ecology of this stream-dwelling species. In a dietary analysis, *S. bealei* was found to assimilate an equal mix of aquatic and terrestrial resources (Sung 2021), suggesting its dependence on both the aquatic habitats and the surrounding riparian forests. Study of the reproductive biology of *S. bealei* identified that their nests are often shallow and covered with soil and leaves, typically within 10 m from the stream bank (Lin et al. 2018). While female *S. bealei* generally prefer to nest close to streams, they have also been observed traveling up to 50 m to search for suitable nesting sites (Lin et al. 2018). Habitat use at the macro level that describes the full spectrum of environmental characteristics, i.e., the geographical range, a species can occupy, has been mapped for *S. bealei* (Hu et al. 2016). Microhabitat selection at the fine-scale level has also been investigated for *S. bealei* (Yuan et al. 2025). Both studies show that *S. bealei* exhibits strong preferences for features that facilitate concealment (e.g., moderate to deep water, stone-dominated substrates, and dense canopy) and foraging efficiency (e.g., greater abundance of fruit and benthic prey). However, an integrated knowledge about the species' spatial ecology, including a hierarchical analysis of habitat selection, remains absent.

Benefiting from the persistence of a few stable populations in Hong Kong, we used radiotelemetry to examine the home range, movement pattern, and habitat use of *S. bealei*. We answered the following questions: (1) What is its spatial distribution throughout the year? (2) Do home range size and movement patterns differ in relation to reproductive class? (3) Does variation in morphological traits influence movement patterns? (4) How do abiotic environmental factors influence movement patterns and habitat use across both seasonal and diel cycles? Answering these questions about the movement pattern and habitat use is fundamental to the understanding of its basic biology, as well as its vulnerability to human-induced environmental changes. We leverage these data to further provide recommendations on its conservation.

2 | Materials and Methods

2.1 | Study System

This study was conducted in a rocky stream within a protected area in Hong Kong, China (22°09′–22°37′N, 113°50′–114°30′E). The study stream is located at 200 m a.s.l. within a secondary forest, and has a mean width of 2.1 ± 1.0 m and water depth of 11.8 ± 12.8 cm. All site-level characteristics were derived from field measurements (see Section 2.5).

Two freshwater turtle species, *Sacalia bealei* and the big-headed turtle (*Platysternon megacephalum*), co-inhabit this stream. Their populations in this stream have been relatively stable despite heavy poaching pressure within the surrounding regions. This presents a rare opportunity for studying the ecology of *S. bealei* in its natural habitat. Despite the relatively undisturbed nature of the stream, we observed a poaching event during the study period. Baited traps were found and one of the telemetered individuals was trapped. All traps were removed and all trapped individuals were released unharmed. With frequent monitoring and remote surveillance enabled by camera traps, we believe this incident represents a one-off event and assume poaching had negligible effects on the behavioral characteristics we investigated. Given the pressing threat of poaching, we do not disclose the exact location of the study stream.

2.2 | Turtle Sampling

We captured *S. bealei* using baited hoop traps following Sung et al. (2013) or by hand through opportunistic encounters. Upon the capture of turtles, we measured straight-line carapace length and plastron length using calipers, body mass using an electronic balance, and determined reproductive class (male, female, or juvenile) by visual examination of the secondary sexual characteristics. As part of a long-term population monitoring program, we marked all captured turtles using a marginal scale notching system developed by Cagle (1939). Individual adults whose carapace length was greater than 60 mm were also marked with a unique PIT tag.

2.3 | Radiotelemetry

We radio-tracked 25 *S. bealei* (12 females, eight juveniles, and five males) from April 2020 to October 2021, which encompasses four biologically relevant seasons (wet season: May–August, mating season: September–October, dry season: November–February, and nesting season: March–April)—these are defined based on the climatic conditions of Hong Kong and findings about the reproductive ecology of *Sacalia* spp. (Fu et al. 2006, 2007; Lin et al. 2018). In Hong Kong, the wet and mating seasons are characterized by warm, humid conditions, and increased precipitation, whereas the dry and nesting seasons experience cooler, drier weather, and reduced rainfall (Supporting Information S1: Table 1).

Throughout the study, we attached radio-transmitters (SOPR-2190, 5.0–6.0 g or SOPR-2038, 1.8–2.1 g; Wildlife Materials International Inc., New York, USA) to the right side of the posterior margin of the carapace of each individual using epoxy putty glue (Figure 1). This unilateral attachment minimizes height obstruction, allowing for a streamlined profile and reducing potential impediments to behaviors (e.g., movement in confined spaces and male mounting during mating). While there may be theoretical concerns regarding impacts on swimming balance or hydrodynamics, we did not observe any adverse influence on turtles' behaviors or swimming abilities. To minimize impacts imposed by tag mass, we controlled the total applied weight to below 5% of the individual's body weight (Kenward 2000).

We radio-tracked individual turtles using a portable telemetry receiver (IC-R10, ICOM Inc., Kirkland, WA) and a handheld 3-element Yagi antenna (Biotrack Ltd., Wareham, United Kingdom). Individuals were relocated twice a week, once during the day and once at night. At each relocation event, we determined the location of each individual through triangulation. At each relocation point, we recorded the date, time, global positioning system (GPS) coordinates (with a fix error rate below 10 m from a handheld GPS device [Garmin GPSMAP® 62 s; Garmin Ltd., Olathe, Kansas, USA]), habitat type, microhabitat features (within a 0.5 m^2 plot surrounding the individual), and the behavior (swimming, basking, underwater, surfacing, or overland) of individual turtles. To avoid bias from handling stress, we excluded data from the first week after release.

Across the study, we encountered two instances where the transmitter antenna became entangled with submerged roots in shallow water. These incidents were promptly addressed. No injuries or fatalities were reported. By the end of the study, we recaptured all turtles and removed all transmitters.

2.4 | Home Range and Movement Patterns

We estimated individual home range using the Minimum Convex Polygon (MCP) method. The MCP method has been one of the most widely adopted methods in estimating home ranges (Powell 2000), and benefits from historical consistency and comparability (Jennrich and Turner 1969). As MCP has been evaluated as a statistically robust home range estimation method for herpetofauna (Row and Blouin-Demers 2006), this method is favored and is persistently applied in telemetric studies of reptiles (Crane et al. 2021). We used a 100% contour for the calculation of individual MCPs using the R package adehabitatHR (Calenge 2011c). A 100% MCP encompasses all relocations of interest and arranges them in an angle no greater than 180° to create the smallest possible convex polygon (Schoener 1981; Worton 1987). We excluded individuals monitored with less than five relocation points from the calculation of MCP.

Given criticisms of the MCP method for overestimating home ranges by including areas not used by the animals (Börger et al. 2006; Laver and Kelly 2008), we additionally calculated 100% stream distance traveled by individual *S. bealei* to account for space use along linear features. This is calculated by finding the shortest path between the two furthest relocation points snapped on the stream network (i.e., stream distance between nodes) and the straight-line distances between each of the nodes and the corresponding relocation points. This was conducted through the sf (Pebesma 2018) and sfnetworks packages (van der Meer et al. 2024) in the R statistical software.

We summarized movement trajectories into mean daily displacement distance by calculating the straight-line distances between successive relocations using the R package adehabitatLT (Calenge 2011a) and dividing it by the number of-days elapsed since the previous relocation. We excluded estimates with a sampling interval longer than 14 days. We summarized daily displacement distances for each individual by averaging it over the entire tracking period and by each season.

2.5 | Habitat Measurement

We characterized habitats into five different types: riffles, runs, pools, open uplands, and forested uplands (Supporting Information S1: Table 2). Additionally, we measured five environmental features, including water depth, stream width, canopy cover, cover of leaf litter, and substrate types, with a 0.5 m^2 sampling quadrat centering on the telemetered animal (Supporting Information S1: Table 3). We selected these microhabitat features that are believed to be linked to the biology of freshwater turtles, such as those that facilitate an individual's ability to thermoregulate, balance energetics, acquire resources, and evade threats.

We did not sample habitat data for individuals that were actively swimming ($n = 14$) or trapped ($n = 2$), as their behavior and habitat use were likely under human influence and may not reflect true preferences. Additionally, when a turtle was spotted basking ($n = 2$), we quantified the habitat use by measuring the aquatic habitat directly adjacent to the basking location.

To test the hypothesis of nonrandom habitat use, we systematically sampled available habitat using a random sampling design from July 2020 to August 2021. Each month, we sampled available habitat every 10 m along the study stream. At each 10-m mark, a random point was selected laterally perpendicular to the stream flow using a randomly generated number (1–100) to denote the percent width (leftmost side = 1; rightmost side = 100). At each random location, we recorded the habitat type and microhabitat features as detailed above.

To evaluate microhabitat use, we paired each relocation point with a random point. The random point was randomly selected from a monthly collection of available habitats, sampled within a random distance from the relocation point. For relocation points that were sampled outside of the major channel of the study stream or sampled in months without a systematic measurement of available habitats (i.e., periods before July 2020 and after August 2021), the paired random locations were directly sampled by traveling a random distance from the relocation point. All random distances were randomly drawn from the interquantile range of distances moved by *S. bealei* between successive locations (i.e., 3–15 m) (Compton et al. 2002). To account for potential GPS fix errors, we included an additional 10 m buffer around each relocation point when selecting the paired random point.

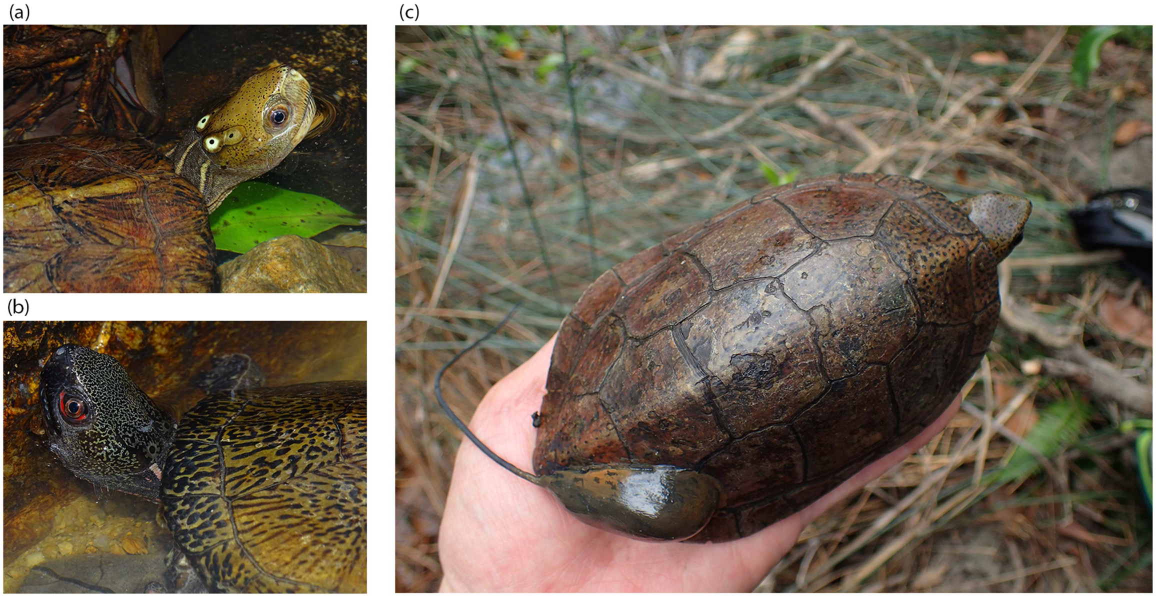

FIGURE 1 | Photographs of (a) an adult female Beale's eyed turtle (*Sacalia bealei*), (b) an adult male, and (c) an individual with a radio-transmitter attached to its carapace.

2.6 | Data Analysis

We fitted linear mixed-effect models (LMMs) to investigate how home range size and movement were affected by season, reproductive class, and body size. We log-transformed 100% MCP for normalization prior to analysis. We included turtle ID as the random effect to account for repeated measurement of the same individual across seasons. Additionally, we included the number of relocation points to control the effect of sampling effort on home range size estimation. We selected the best model using a backward selection process, starting with a global model that consisted of all fixed terms, a multiplicative effect that assessed the reproductive dynamics across seasons (reproductive class × season) and a multiplicative effect that examined the thermoregulatory dynamics in relation to allometric scaling (body size × season). Models were fitted using the lme4 package (Bates et al. 2014) in R. We examined the significance of individual terms using likelihood ratio tests with the car package (Fox and Weisberg 2019). Model assumptions were validated using the DHARMa package (Hartig and Hartig 2017).

Annual and seasonal habitat selection were investigated using a hierarchical framework (Johnson 1980). At the landscape level, habitat was selected during the initial establishment of a home range and was explained primarily by the regional habitat composition. Here, we focused on habitat selection at local scales: the second- and third-order habitat selection. Habitat selection refers to the habitat that a species disproportionately uses more frequently than would be expected given the relative availability of other habitat resources (Johnson 1980). At each spatial scale, we compared used and available habitats to test if *S. bealei* selected habitat disproportionately through compositional analysis (Aebischer et al. 1993) using the adehabitatHS package (Calenge 2011b) in R. We studied second-order habitat selection by considering preferential use of habitat at the population range, where we compared the proportions of each habitat type sampled within the home range of all surveyed turtles to those sampled within an individual's home range. At the third-order habitat selection, preferential habitat use was studied at the home range level by comparing the habitat type proportions sampled within an individual's home range to those that were selectively used by the respective individual.

During the compositional analysis, we calculated the log ratios of used and available habitats with the formulae $y_i = \ln(x_i/x_j)$, where x_i is the proportion of habitat type i and x_j is the proportion of the reference habitat. We arbitrarily selected the riffle as the reference habitat. If habitats are randomly selected by *S. bealei*, the log ratios of used habitat (y_u) should be similar to the log ratios of the available habitats (y_a), and the vector of differences ($d = y_u - y_a$) should not be significantly different from zero. We thereby tested the null hypothesis of $d = 0$ for each spatial scale and for each season using a one-sample t-test or a Wilcoxon test when the assumption of multivariate normality was violated. To provide a better spatial representation given infrequent relocations, we included a 15 m buffer when defining the population and individual home ranges.

Resource selection functions (RSF) were used to assess the microhabitat requirements of *S. bealei*. By pairing each used location with an available location, RSF investigated if microhabitat features differed between the used and available locations using binomial Generalized Linear Mixed Models (GLMMs). This allowed identification of features that explain the preferential microhabitat use of *S. bealei*. During analyses of microhabitat selection, it is important to consider both non-linear patterns of microhabitat use and functional response between different environmental conditions and microhabitat use (Fieberg et al. 2021); we therefore included all microhabitat features with quadratic polynomials and the interaction between each microhabitat feature and season as predictors of the global model. To further account for intraspecific variation in the animal's spatial behaviors, we investigated microhabitat selection following Muff et al. (2020)'s approach, which involves fitting a mixed logistic regression model with individual identity modeled as random slopes to the predictor variables. All models were fitted using the glmmTMB package (Magnusson et al. 2017) in R. The best-fitting models were selected using a backward selection process. We standardized all predictors of continuous values prior to the analysis. Additionally, to avoid issues related to multicollinearity, we removed strongly correlated variables (i.e., variance inflation factors, VIFs >3, Zuur et al. 2010) from subsequent analyses, that is, cover of boulder substrate.

3 | Results

We radio-tracked 25 *Sacalia bealei* (12 females, eight juveniles, and five males) for at least 2 consecutive months (mean ± SD = 284 ± 104 days, range = 69–486 days). Greater movement, as indicated by a larger home range, was observed in both the wet (May–August) and mating seasons (September–October) (Supporting Information S1: Figures 1, 2). In these seasons, males tended to travel a longer distance and covered a larger home range than females and juveniles. From the dry season (November–February) onward, home range and movement of all individuals were reduced and remained low through the nesting season (March–April) (Supporting Information S1: Figures 3, 4).

The average 100% MCP and stream distance measured across individuals were 7986 ± 9701 m^2 and 261.7 ± 197.3 m, respectively. The averaged daily displacement distance was 4.7 ± 8.9 m. Model results indicate a statistically significant seasonal shift in average daily displacement distance, with individuals exhibiting greater displacement distance during the wet season (7.0 ± 11.1 m) and mating season (5.1 ± 9.6 m) compared to the dry season (2.8 ± 5.7 m; $t_{\text{wet–dry}(66)} = 6.081$, $p_{\text{wet–dry}} < 0.001$; $t_{\text{mating–dry}(63)} = 3.590$, $p_{\text{mating–dry}} = 0.004$) and nesting season (3.2 ± 7.2 m; $t_{\text{wet–nesting}(64)} = 5.959$, $p_{\text{wet–nesting}} < 0.001$; $t_{\text{mating–nesting}(61)} = 3.321$, $p_{\text{mating–nesting}} = 0.008$). In the wet and mating seasons, there was a significant relationship between reproductive class and daily distance traveled ($\chi^2_6 = 40.886$, $p < 0.001$). Males exhibited significantly greater daily displacement distances (wet season: 14.5 ± 17.3 m; mating season: 13.3 ± 17.5 m) than that of females (wet season: 4.8 ± 7.5 m; $t_{\text{male–female}(49)} = 6.694$, $p_{\text{male–female}} < 0.001$; mating season: 3.2 ± 5.1 m, $t_{\text{male–female}(70)} = 4.474$, $p_{\text{male–female}} < 0.001$) and juveniles (wet season: 5.8 ± 8.5 m; $t_{\text{male–juvenile}(56)} = 5.353$, $p_{\text{male–juvenile}} < 0.001$; mating season: 4.3 ± 7.5 m, $t_{\text{male–juvenile}(73)} = 3.250$, $p_{\text{male–juvenile}} = 0.005$) (Figure 2).

For home range size, there were significant additive effects of reproductive class ($\chi^2_2 = 8.805$, $p = 0.012$) and season ($\chi^2_3 = 15.031$, $p < 0.001$) on the 100% MCPs. The MCP of males (22,180 ± 10,888 m^2) was significantly larger than that of females (5380 ± 5653 m^2; $t_{19} = 2.921$, $p = 0.023$). There were no significant differences between the MCPs of females and juveniles ($t_{26} = -0.374$, $p = 0.926$) or that of males and juveniles ($t_{26} = 2.180$, $p = 0.095$) (Figure 3). Home range size differed significantly across seasons, with MCPs being larger during the warmer period (wet season: 3992 ± 7026 m^2; mating season: 2398 ± 5469 m^2) when compared to those during the cooler period (dry season: 1297 ± 2825 m^2, $t_{\text{wet–dry}(71)} = 4.212$, $p_{\text{wet–dry}} < 0.001$, $t_{\text{mating–dry}(74)} = 3.420$, $p_{\text{mating–dry}} = 0.006$; nesting season: 1384 ± 3553 m^2,

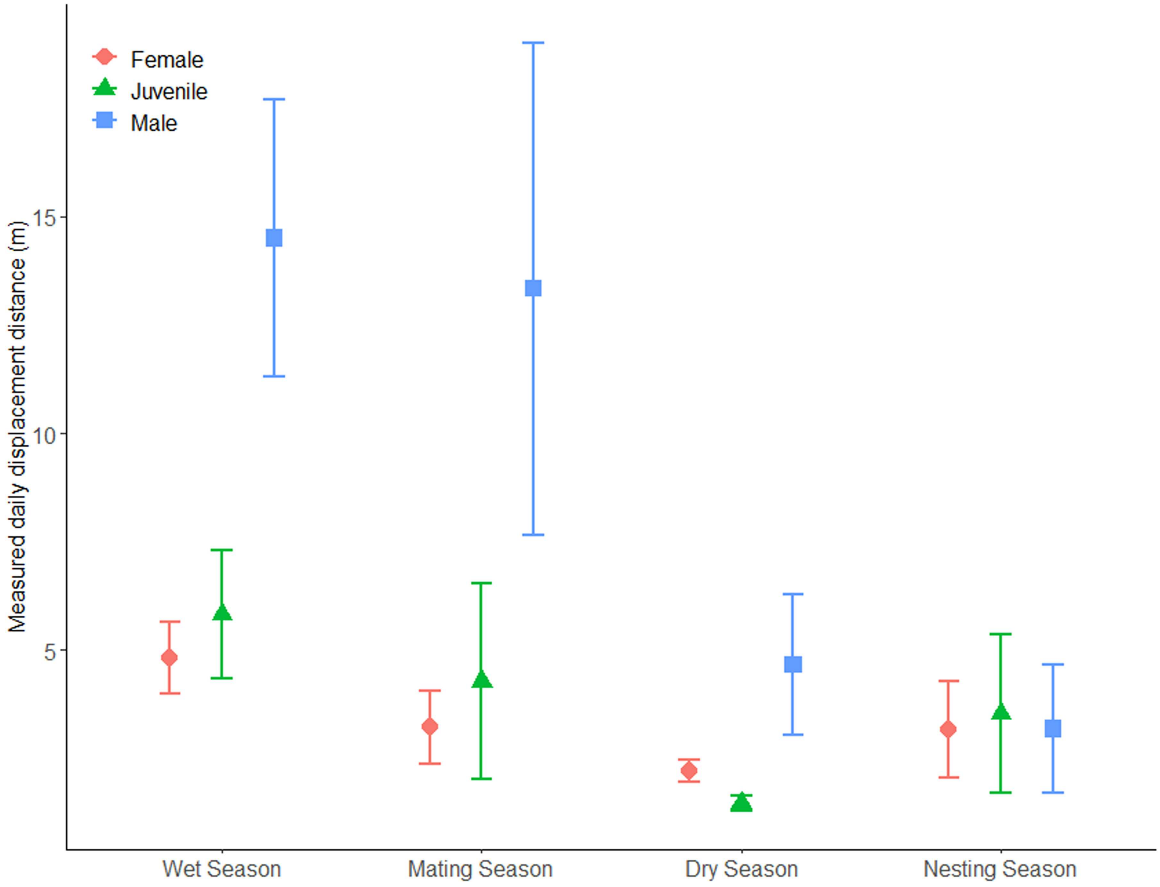

FIGURE 2 | Average daily displacement distance (m, mean ± SD) measured for 12 females (•), eight juveniles (▲), and five males (■) of the Beale's eyed turtle (*Sacalia bealei*) in the wet season (May–Aug), mating season (Sept–Oct), dry season (Nov–Feb), and nesting season (Mar–Apr).

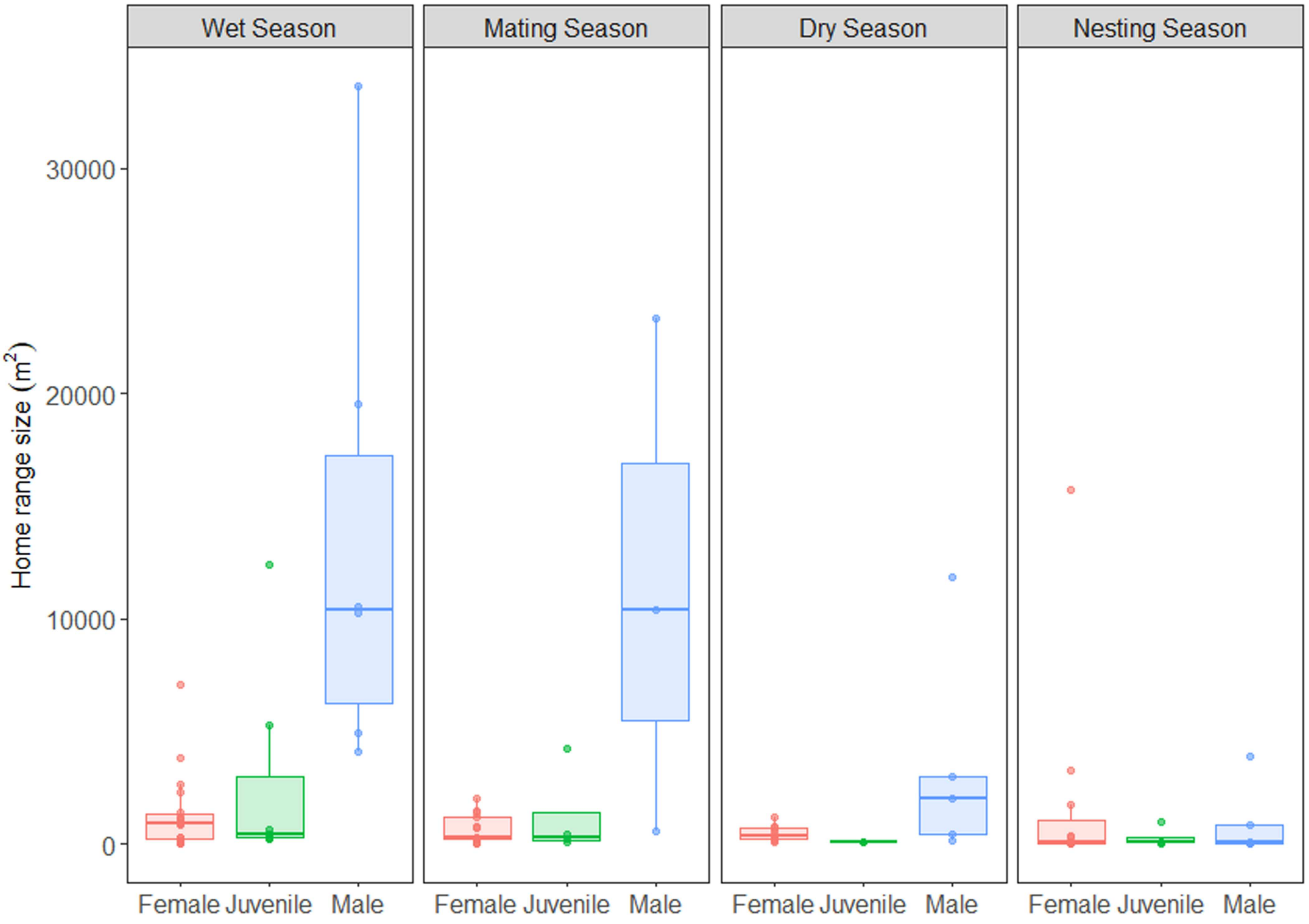

FIGURE 3 | Boxplot showing home range size (m^2) estimated using 100% Minimum Convex Polygons (MCPs) for the Beale's eyed turtle (*Sacalia bealei*) during the wet season (May–Aug), mating season (Sep–Oct), dry season (Nov–Feb), and nesting season (Mar–Apr).

$t_{\text{wet–nesting}(66)} = 3.689$, $p_{\text{wet–nesting}} = 0.003$, $t_{\text{mating–nesting}(67)} = 3.555$, $p_{\text{mating–nesting}} = 0.004$) (Figure 3).

Among the 1663 relocations, terrestrial habitat use (19 relocations, ~1%) was rare. The observed terrestrial movement was mostly made by three adult females during the mating season from August to October, except one occasion in mid-July attempted by an adult male. Given the highly aquatic nature of *S. bealei*, we tested for the nonrandom use of aquatic habitats at two spatial scales using compositional analysis following a hierarchical order. At the second-order habitat selection, turtles exhibited nonrandom selection of the habitat types in their home ranges from those in the population range (Wilk's $\lambda_2 = 0.600$, $p = 0.002$), with turtles preferring pools ($t_{24} = 3.766$, $p < 0.001$) and riffles ($t_{24} = 3.013$, $p = 0.006$) over runs (Figure 4a). At the third-order habitat selection, *S. bealei* selected the habitats within their home ranges nonrandomly (Wilk's $\lambda = 0.493$, $p < 0.001$), with turtles preferentially selecting pools over the other habitat types ($W_{\text{pool-run}} = 309$, $p_{\text{pool-run}} < 0.001$; $W_{\text{pool-riffle}} = 292$, $p_{\text{pool-riffle}} < 0.001$) (Figure 4b).

RSFs showed that microhabitat selection was significantly influenced by water depth, substrate cover, cover of leaf litter, and canopy cover (Figure 5). For these variables, we discovered seasonal and diel variation in the microhabitat use of *S. bealei*. In general, *S. bealei* was more likely to select areas with greater water depth (local maxima of the *p.d.f.* > 60 cm) in the wet season, whereas they preferred shallower water (local maxima of the *p.d.f.* = 30–40 cm) during the cooler periods in dry (at night only) and nesting seasons (Supporting Information S1: Figure 6). The dominant types of substrate cover in used habitats were gravel (34.8% ± 28.0%) and boulder (55.8% ± 30.6%). In general, *S. bealei* preferred areas with greater structural cover, such as crevices or caves formed between boulders (W. S. Chan, pers. obs.), which were associated with lower covers of pebble and cobble (Supporting Information S1: Figure 12). This is marked by significant negative associations with the use of pebbles during the dry and nesting seasons (Supporting Information S1: Figure 8). Meanwhile, there was no clear pattern in the selection of pebble and cobble covers during other periods, except during the wet season in 2020 (Supporting Information S1: Figures 8, 9). *S. bealei* generally selected areas with low leaf litter cover (8.8% ± 18.0%). Yet, *S. bealei* selected areas with greater leaf litter cover during nighttime in mating and dry seasons (Supporting Information S1: Figure 10); whereas their preference for selecting leaf litter cover dropped dramatically during the nesting period, regardless of the time of day (Supporting Information S1: Figure 10). Daytime microhabitat use by *S. bealei* was strongly influenced by

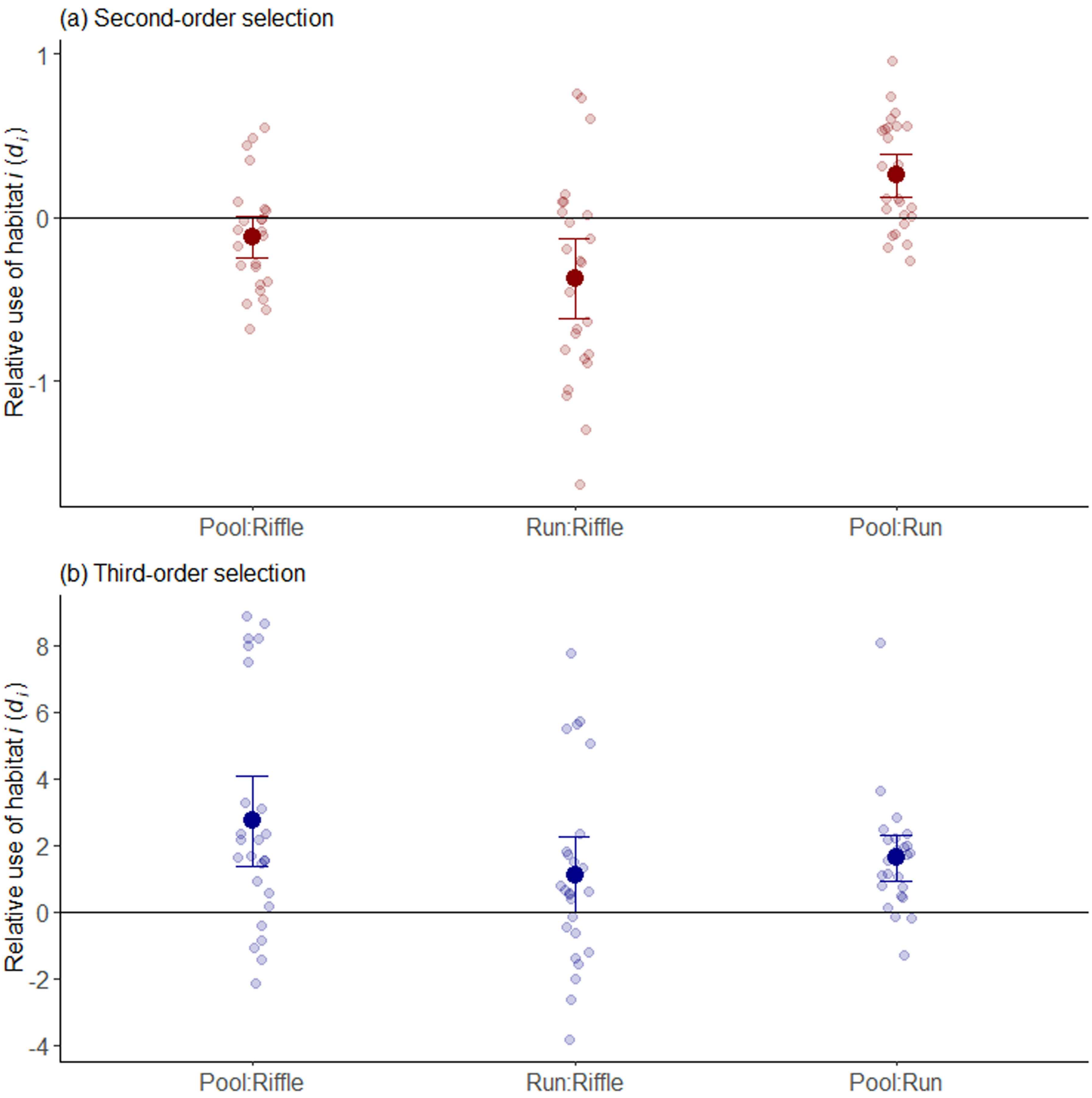

FIGURE 4 | Nonrandom use of aquatic habitats in the Beale's eyed turtle (*Sacalia bealei*) among three habitat types (pool, run, riffle). (a) Second-order selection corresponds to the relative use of habitat types i (d_i, mean ± 1.96*SE) in relation to their availability within the population range. (b) Third-order selection corresponds to the relative use of habitat type i (d_i, mean ± 1.96*SE) in relation to their availability within the 100% minimum convex polygon (MCP). Random habitat use, indicated by the horizontal line where $d_i = 0$, shows no selection between habitat pairs.

canopy cover, with selection probabilities peaking either at moderately exposed areas (20%–60%) or highly shaded areas (90%–100%) (Supporting Information S1: Figure 11).

4 | Discussion

In this study, we radio-tracked wild *Sacalia bealei* to understand their movement and space use patterns. *S. bealei* exhibited larger home ranges than the sympatric *Platysternon megacephalum*. Both home range size and movement patterns of *S. bealei* exhibit sex- and season-specific variations. Habitat use was predominantly aquatic, with a specific preference for step-pools. *S. bealei* also showed preferences for various microhabitat features, with distinct seasonal and diel variations.

4.1 | Home Range and Displacement Distance

Home range (100% MCP = 7986 ± 9701 m^2, 100% stream distance = 261.7 ± 197.3 m) and movement (4.7 ± 8.9 m day^{-1}) of *S. bealei* are substantially larger than those of the sympatric *P. megacephalum* (100% MCP = 996 m^2, 100% straight-line distance = 97 m; daily displacement distance = 0.5–2.2 m day^{-1}, Sung et al. 2015). The relatively large spatial extent of *S. bealei*, in addition to its dependence on aquatic habitats (see section below), highlight its sensitivity to the loss of stream habitats. Any adverse changes to the stream ecosystem may thus hinder their reproductive and foraging success (Hinam and Clair 2008).

The reproductive strategies hypothesis has been proposed as a general paradigm to explain the differential movement patterns between reproductive classes in semi-aquatic turtles (Morreale et al. 1984). The hypothesis predicts that males exhibit higher

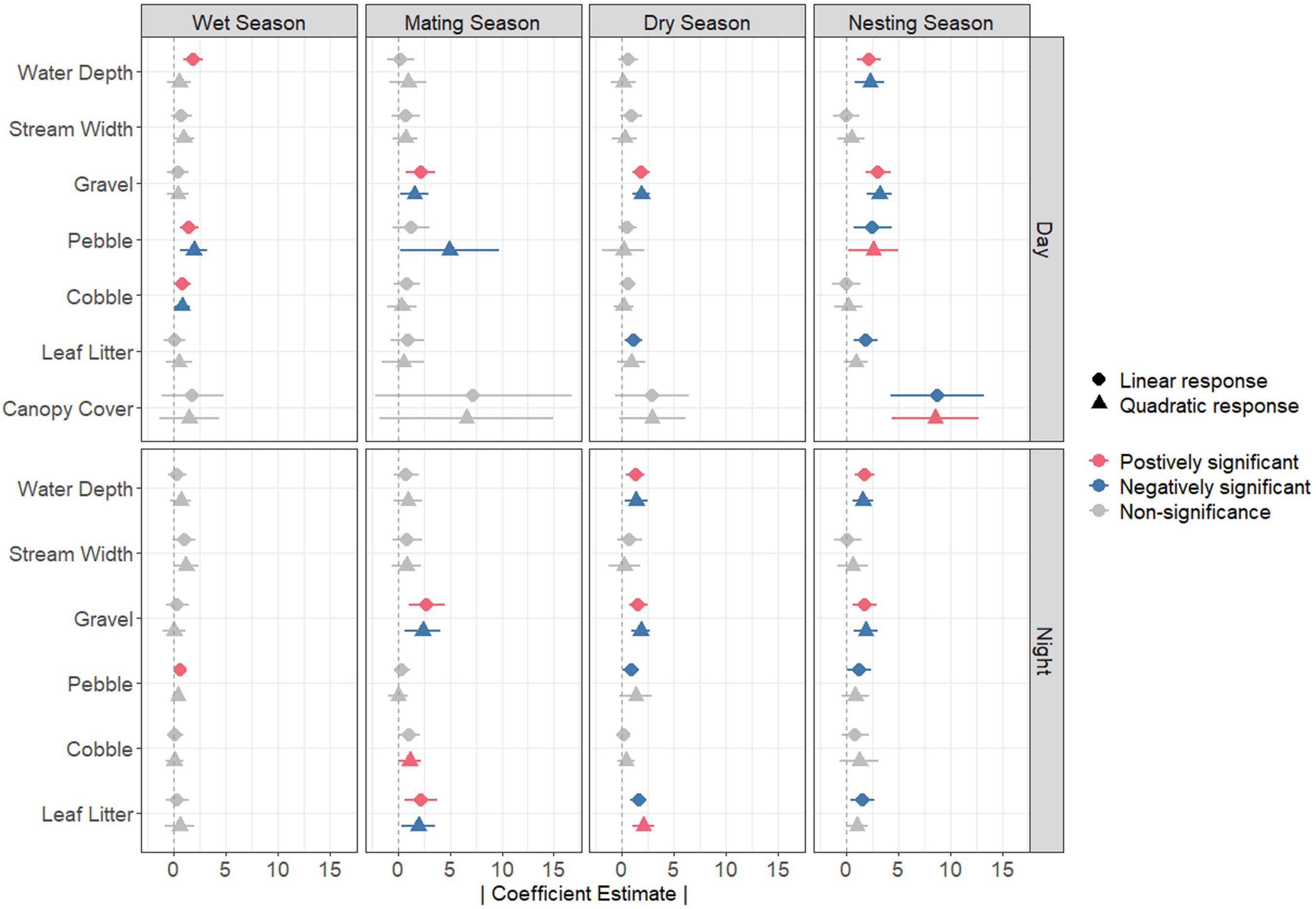

FIGURE 5 | Seasonal and diel microhabitat selection by the Beale's eyed turtle (*Sacalia bealei*). The strength of the microhabitat use pattern was represented by the absolute value of the conditional beta coefficient (|mean| ± SE) estimated from the resource selection function (RSF). Microhabitat use patterns were evaluated with both linear (•) and quadratic (▲) functions. Significant microhabitat use ($\alpha = 0.05$) was indicated by colored points, with red indicating a positive effect and blue a negative effect. Models correspond to the full model with turtle ID included as a random slope to the predictor variables.

levels of movement and greater spatial extent than females in exchange for enhanced fitness as a result of mate-seeking behaviors (Morreale et al. 1984; Gibbons 1986). Studies of the hypothesis in freshwater turtles have yielded mixed results—some indicate greater movement in adult males compared to females (e.g., Stone et al. 2015; Van Dyke et al. 2023), while others report negligible effects (e.g., Sung et al. 2015; Kong et al. 2021) or the reverse (e.g., Doody et al. 2002; Carrière et al. 2009). Despite the variability, our results on *S. bealei* accord with the hypothesis. Since female *S. bealei* in the study population aggregated across various stream sections, males likely expanded their home ranges to gain access to multiple mating partners. Such sex-specific differences in movement and home range behaviors of *S. bealei* were significant only during the wet and mating season, which resembles research conducted on *Sacalia quadriocellata* (Fu et al. 2007).

Sex-specific spatial behaviors highlight distinct vulnerabilities between sexes to threats such as poaching and habitat loss. Compared with females, males—whose home ranges are larger—face a higher risk of poaching, as they traverse extensive areas that may more easily intersect with illegal trapping activities, even if these efforts are concentrated in a short section of a stream. Indeed, the female-biased sex ratios (M:F ratio = 1:1.6–3.7; Y. H. Sung & W. S. Chan, unpublished data) observed across local remnant populations could be indicative of past and ongoing poaching pressure. Conservation strategies should, therefore, focus on protecting locations with remnant populations and prioritize monitoring during wet and mating seasons when males expand their movement ranges.

Home range and movement of *S. bealei* also varied seasonally, likely reflecting physiological limits and resource availability. As ectotherm activity depends largely on temperature (Huey 1982), lower temperatures during the dry and nesting seasons may constrain their movement. Meanwhile, increased activity in the wet and mating seasons coincides with periods of increased food availability, for example, *Machilus chekiangensis* fruits (April–May) and terrestrial insects (Sung et al. 2021).

4.2 | Habitat Preferences

We found that *S. bealei* relies strongly on aquatic habitats. This suggests that interstream dispersal is likely limited, which could expose them to greater risk of local extirpation (Alacs et al. 2007). As poachers mainly deploy traps underwater, the highly aquatic nature of *S. bealei* also increases its vulnerability to poaching. This stresses the importance of enhanced protection and patrolling along streams for *S. bealei* and other freshwater turtles in Hong Kong (Sung et al. 2015). In particular, the selective preference of *S. bealei* for pool habitats (third-order habitat selection) interspaced between repeating sequences of riffles and pools (second-order habitat selection) underscores the need to prioritize conservation measures around step-pool systems, such as setting up surveillance cameras or planning patrol routes around those habitats.

The docile nature and lack of defensive mechanisms in *S. bealei* suggest that selecting microhabitats that offer protection against potential threats and predators is vital to its survival. This may explain its general preferences for deeper water and substrata that facilitate hiding. For example, the selection of substrate types (other than the general preference for gravel) is mostly random and represented by a mix of rocky substrates that facilitate avoidance behaviors either through refuge seeking under boulders (Hu et al. 2016; Yuan et al. 2025) or masquerading as pebbles and cobbles (Xiao et al. 2016, 2020). This study ascertains that having multiple habitat features that facilitate hiding behaviors could be a primary driver underlying the spatial requirements of *S. bealei* (Yuan et al. 2025). This emphasizes the critical importance of reinforcing habitat structures that support concealment when planning for ex-situ conservation or reintroduction programs.

Additionally, to balance trade-offs between threat avoidance and physiological functioning, thermally favorable environments (i.e., sparse canopy cover) selected by *S. bealei* were typically associated with features that facilitate hiding (i.e., increased water depth and greater boulder cover; Supporting Information S1: Figure 12). Conversely, selection of resource-rich areas (i.e., dense canopy cover) was mostly accompanied by more pebbles and cobbles, which encourage masquerading behaviors in a shaded environment (Supporting Information S1: Figure 12). Our findings highlight the importance of considering the relative significance of various habitat characteristics that may collectively impact the habitat selection process.

Microhabitat preferences also differ across seasonal and diel cycles. Seasonal variation in temperature and precipitation corresponds with shifts in *S. bealei*'s water depth preferences, likely reflecting adaptations for locomotor efficiency and energy use. During the wet season, when spates occur, preference for deeper water may represent a strategy to avoid displacement by strong surface currents (Jones and Sievert 2009). Meanwhile, during cooler periods, preference for shallow-to-intermediate water may suggest a thermoregulatory strategy to exploit warmer temperatures near the water surface (Chessman 2024). Staying near the surface may also minimize energetic costs associated with swimming (Stokes et al. 2023) and surfacing (Feder and Moran 1985). Seasonal and diel variations in food availability may explain the variability in *S. bealei*'s associations with leaf litter cover. *S. bealei* selected more heavily for leaf litter cover during nighttime in months following the wet season when food resources become less abundant. Assessing how microhabitat preferences vary both spatially and temporally can facilitate a better understanding of species-habitat relationships and inform effective conservation planning.

Although our study was limited in scope (i.e., a single population in Hong Kong with a strongly female-biased population) and duration (i.e., mostly 1 year of individual sampling given constraints on the size of the transmitter), our work provides the largest available movement dataset for *S. bealei* and advances knowledge of its habitat and microhabitat preferences. Future work should expand the spatial and temporal scales of data collection pertaining to the animal's habitat use.

4.3 | Conservation Implications

The global depletion of freshwater turtles is a critical and urgent conservation issue. Through radiotelemetry, we provide baseline information on the movement behaviors of *S. bealei*, one of the rarest stream-dwelling freshwater turtles endemic to southeastern China. We found that *S. bealei* exhibits larger home ranges and more extensive movements than its sympatric counterpart, highlighting its sensitivity to the loss or degradation of stream ecosystems. This, coupled with the species' susceptibility to poaching due to its strong association with aquatic habitats, underscore the need for enhanced protection of streams, particularly around step-pool systems where *S. bealei* predominantly selects. Despite seasonal and diel variations in microhabitat selection, *S. bealei* generally prefers spatial elements that provide concealment either through hiding in deep water, sheltering under rocks, or masquerading as pebbles and cobbles. This suggests that concealment is a primary spatial requirement of *S. bealei* and should be considered when planning for ex-situ conservation programs. However, *S. bealei*'s general aversion to leaf litter cover—which offers an effective barrier to visual and tactile inspection—could increase its chances of being detected even in the absence of traps. This study, therefore, highlights not only the importance of regular patrols to detect trapping devices but also the need to identify suspicious activities. To protect the few remaining localized populations, patrolling efforts must be strengthened urgently.

Author Contributions

Wing Sing Chan: conceptualization, methodology, software, data curation, investigation, formal analysis, visualization, writing – original draft, writing – review and editing. **Jonathan J. Fong:** methodology, funding acquisition, writing – review and editing, project administration, conceptualization. **Timothy C. Bonebrake:** conceptualization, methodology, validation, supervision, project administration, resources, writing – review and editing, software. **Yik-Hei Sung:** writing – review and editing, conceptualization, methodology, data curation, validation, supervision, funding acquisition, visualization, project administration, resources.

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Ethics Statement

All sampling procedures were approved by the Department of Health (Ref no: (19-77) in DH/HT&A/8/2/8 Pt.1 and (22-1) in DH/HT&A/8/2/8 Pt.3), and Agriculture, Fisheries, and Conservation Department (Ref

no: (3) in AF GR CON 09/51 Pt.8 and (86) in AF GR CON 09/51 Pt.7.) of Hong Kong SAR Government.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw tracking dataset generated during the current study is not publicly available due to conservation concerns, but it is deposited at the Movebank data repository (Movebank Study ID 5056848767) and can be made available by the author upon reasonable request. All summarized datasets and codes used in the current study are publicly available at https://github.com/wingsingChan/SABE_Radiotelemetry_Public.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.
Supplementary File: wll270037-sup-0001-SABE_Radiot0065lemetry_manuscript_SI.docx.