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CLEMENCE ALLEMAN[1,2], JEAN-FRANÇOIS GERARD[3], MADEN LE BARH[1], REMI HELDER[1], GILLES FRONTEAU[2], EMMA SALVO[1], PAULINE HUBERT[1]

[1]Université de Reims Champagne-Ardenne – Centre de Recherche et de Formation en Éco-éthologie (URCA-CERFE), 5 Rue de la Héronnière, 08240 – Boult-aux-Bois, France.

[2]Université de Reims Champagne-Ardenne – Groupe d'Étude sur les Géomatériaux et Environnements Anthropisés (URCA-GEGENA), UR 3795 – UFR SEN, 2 esplanade Roland Garros, 51100 – Reims, France.

[3]Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement – Comportement et Écologie de la Faune Sauvage (INRAE-CEFS), 24 Chemin de Borde Rouge, 31320 – Auzeville-Tolosane, France.

**Corresponding author.* Email: clemence.alleman@gmail.com

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Abstract. Most amphibians rely on both aquatic and terrestrial environments throughout their life cycle. While the use and selection of aquatic habitats are well documented in many species, terrestrial habitats remain far less studied. The yellow-bellied toad (*Bombina variegata*) is a small, cryptic species whose terrestrial ecology is poorly known, particularly regarding the use and selection of resting sites. To address this gap, we tracked 31 individuals using VHF transmitters during the breeding and post-breeding seasons, and characterized their terrestrial shelters. These shelters were used occasionally during the breeding season, either as resting sites near aquatic habitats or during movements, and more intensively after the breeding season, possibly in preparation for wintering. Shelters were found across a wide range of microhabitats, with selection primarily driven by the presence of holes and high woody debris cover. Distances between terrestrial shelters and the aquatic sites used varied greatly among individuals, highlighting the importance of maintaining suitable terrestrial habitats within several hundred meters around aquatic sites. This study emphasizes the importance of considering terrestrial microhabitats in forest management for the conservation of this species.

Key-words. *Bombina variegata*, radio telemetry, habitat selection, terrestrial shelter, conservation

INTRODUCTION

Most amphibians have multiple life stages that involve alternating between aquatic and terrestrial environments (Liedtke et al., 2022; Nolan et al., 2023). The terrestrial ecology of amphibians remains under-documented compared to their aquatic ecology, particularly with regard to habitat use and selection (Gibbons, 2003; Burrow and Maerz, 2022). However, this habitat plays a crucial role in several stages of their life cycle (Semlitsch and Bodie, 2003).

Some studies have highlighted the importance of terrestrial environments, for example for foraging, both in predominantly terrestrial urodeles such as salamanders (Feder and Londos, 1984) and in many anuran species including pond-breeding taxa (Toft, 1980; Kolenda et al., 2019). Terrestrial habitats play a key role in amphibian movement, providing corridors that facilitate migration and dispersal (Gibbons, 2003), and the importance of designating and preserving buffer zones and terrestrial corridors around wetlands has already been documented through numerous studies (Semlitsch, 1998; Bulger et al., 2003; Rothermel, 2004; Daversa et al., 2012). In addition, terrestrial environments may also serve as temporary resting sites, refuges during extreme environmental conditions, or seasonal habitats during summer and winter (Keen, 1979; Jaeger, 1980; Forti et al., 2022). Some studies focusing on terrestrial habitats have specifically addressed the selection of terrestrial refuges across different periods of amphibian activity. Madison (1997) reported the use of small mammal burrows as terrestrial refuges by *Ambystoma maculatum* (Shaw, 1802), particularly during winter or extreme weather events such as snowstorms. Similarly, Richter et al. (2001) showed that *Lithobates sevosus* (Goin and Netting, 1940) uses underground shelters during the post-breeding season, including mammal burrows, as well as features associated with fallen trees such as stump holes and root mounds. In another species, *Speleomantes strinatii* (Aellen, 1958), authors also highlighted the importance of fallen wood, especially for shelters located far from streams (Rosa et al., 2025).

Finally, other studies have documented the use of diurnal shelters during activity periods, for example in *Rhinella marina* (Linnaeus, 1758), in which refuge selection varies seasonally but consistently favors protection against desiccation (Schwarzkopf and Alford, 1996), or in *Alytes obstetricans* (Laurenti, 1768), which selects shelters characterized by moist substrates and moderate temperatures (Lange et al., 2020). However, these studies on resting sites selection remain marginal, mainly due to the difficulty of detecting most species during their terrestrial phase (Dodd, 2009; Glover et al., 2023; Koch et al., 2025). This represents an obstacle to conservation, as effective measures cannot be developed for something that is not yet fully understood. This is particularly true for the Yellow-bellied toad (*Bombina variegata,* Linnaeus, 1758), for which an entire component of its biphasic life cycle remains poorly understood.

Indeed, the use and selection of aquatic habitats by the Yellow-bellied Toad are well documented (Beshkov and Jameson, 1980; Barandun and Reyer, 1997; Gollmann et al., 2000; Di Cerbo, 2001; Pichenot, 2008), but substantial gaps remain in our knowledge of terrestrial habitat use during both breeding and post-breeding seasons. This small pond-breeding toad presents cryptic dorsal coloration (Preißler et al., 2021) that blends with the substrate and, combined with its small body size, makes it largely undetectable on land. Only a few studies report occasional and opportunistic observations of individuals in terrestrial environments (Beshkov and Jameson, 1980; Di Cerbo, 2001; Pichenot, 2008), and no studies have specifically examined terrestrial habitat use in this species, particularly the selection of terrestrial shelters. This aspect may therefore be inadequately considered in conservation planning.

Through this study, we aimed to enhance understanding of the use and selection of terrestrial shelters by the Yellow-bellied Toad during the breeding and post-breeding seasons, using radio-telemetry. Specifically, our objectives were to (i) quantify and compare shelter use between the two seasons (ii) identify the main characteristics of shelters selected by individuals, and (iii) describe the distances between aquatic sites and selected terrestrial shelters. Based on opportunistic observations from capture-recapture studies, we expected terrestrial shelters to be used occasionally during the breeding season (Gollmann et al., 2000; Di Cerbo, 2001), and more intensively during the post-breeding season. Given the importance of avoiding desiccation, and as reported for other species, we hypothesized that selected shelters would maintain moisture (Richter et al., 2001; Hinderer et al., 2021; Burrow and Maerz, 2022), and would therefore primarily consist of tunnels and cracks in humus or decaying wood (Pichenot, 2008; Le Barh and Alleman, 2023). Finally, we expected individuals to remain close to aquatic sites during the breeding season, with distances of only a few meters, whereas movements to terrestrial shelters during the post-breeding season were expected to range from a few meters to several hundred meters (Beshkov and Jameson, 1980; Pichenot, 2008; Le Barh and Alleman, 2023).

MATERIAL AND METHODS

Study area

The study was carried out in a forested landscape in the Meuse department, northeast France (Forêt Domaniale de Beaulieu; 49°02’39” N, 5°03’20” E; Fig. 1). With an elevation ranging from 180 to 297 above sea level, the study area covered approximately 630 ha of sessile oak (*Quercus petraea*) and beech (*Fagus sylvatica*) deciduous forest. The aquatic sites for capturing individuals were selected based on previous monitoring data (Le Barh and Alleman, 2023), and consist of fifteen small ponds or ruts.

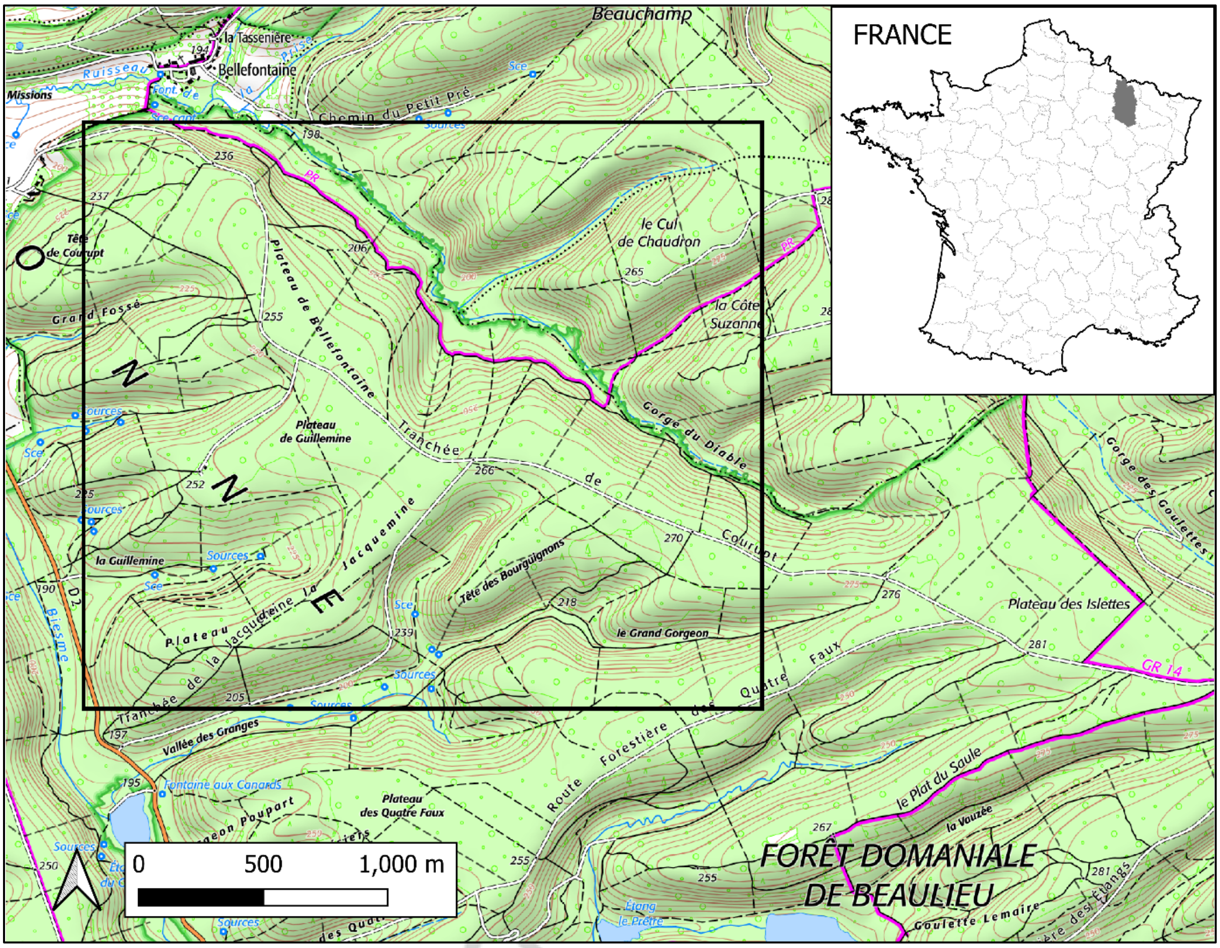

Fig. 1. Study area (black square) in the Meuse department (grey), France.

Capture and equipment

The fieldwork was conducted in 2024 over three sampling sessions, two during the breeding season (from May 14 to June 8 and July 9 to 31) and the last after the breeding season (from September 11 to October 2). At the beginning of each session, individuals encountered at aquatic sites were captured and weighed to ensure they met the minimum mass required for transmitter attachment. Only individuals weighing at least 5g were equipped, in accordance with the guideline that tracking devices should not exceed 10% of an individual's body mass (HACC, 2004). The tracking equipment consisted of a VHF transmitter (BD-2X, Holohil Systems Ltd.) attached using a nylon wire loop enclosed in a silicone sheath, with a total mass of 0.45g ± 0.05 g. The loop was fitted by passing the hind legs through it, positioning the transmitter around the waist like a belt. Handling time was kept to a minimum, and individuals were monitored during transmitter attachment for signs of stress and after fitting to ensure normal locomotor behavior (e.g., jumping, walking, swimming).

Monitoring and shelter characterization

Over the three sampling periods, 31 individuals were tracked twice a day (every twelve hours) using a receiver (Yaesu FT818-ND) and an antenna (3 element folding antenna, Wildlife Materials). The location of each individual was recorded with a Garmin® GPS (GPSMAP 64s). When an individual was located in the terrestrial habitat, hidden and completely immobile (no escape behavior except in case of significant disturbance), we considered it to be in a terrestrial shelter (TS). Conversely, an individual in the terrestrial habitat, visible on the substrate and mobile (even without significant disturbance), was considered to be moving and therefore not in a terrestrial shelter. Once an individual was located in a TS, physical characteristics of the shelter were assessed in the field within a 1-m diameter area centered on the toad's location (Hinderer et al., 2021): presence/absence of water, holes and herbs, woody debris cover (proportion of ground covered), tree and shrub cover (proportion of sky hidden), slope and distance to water. The same characteristics were subsequently recorded at a random location within a 5-m radius of the selected point (generated with QGIS v.3.0), considered as theoretically available and accessible habitat.

Statistical Analyses

First, we compared terrestrial shelter use between breeding and post-breeding seasons by examining the proportion of locations in TS and the average number of times the same shelter was used. We added up individual data to obtain the total number of locations that were or were not shelters for each season, then computed Pearson's χ^2 on the resulting 2x2 contingency table. Afterwards, the test's P-value was estimated using random permutations (Manly, 2007). Each elementary permutation consisted in randomly reassigning season labels (i) between individuals for toads observed during a single season, and (ii) within each individual for toads observed during both seasons. The corresponding 2x2 contingency table and χ^2 were then re-computed. The same operation was carried out 9,999 times, giving us 9,999 values for the χ^2 statistic under the null hypothesis that seasons did not differ. These 9,999 values and the actual value were then combined, and the proportion of the 10,000 values that were higher than or equal to the actual value was taken as the test's P-value. A similar procedure was used to test the difference between seasons in the average number of times the same shelter was used. In this case, after adding up individual data, we calculated for each season the ratio between the total number of locations in shelters and the total number of different shelters, and our statistic was the absolute value of the difference between the two seasonal ratios. The P-value of the statistic under the hypothesis that seasons did not differ was then estimated as previously, using 9,999 random permutations of season labels, re-computing the statistic in each case, then taking the proportion of values (actual value included) that were higher than or equal to the actual value.

Second, we analyzed the factors involved in habitat selection using general linear mixed-effect models (GLMMs; family: binomial; link function: logit) in which the response variable ('Y') was binary, taking value 1 for an actual shelter and 0 for a random location. All models included two random-effect variables, i.e. the individual's identity ('id') and a factor ('site') indicating which random location was paired with which shelter. In a first step, the models considered were fitted to the habitat selection data of a single season, and derived from full model 'A':

$$Y \sim \textit{woody debris cover} + \textit{tree cover} + \textit{shrub cover} + \textit{water} + \\ \textit{hole} + \textit{herbs} + \textit{slope} + (1|\textit{id}) + (1|\textit{site})$$

In this model, fixed-effect variables were the characteristics recorded for the different shelters and random locations, once transformed into binary or categorical variables (Table 1).

Full model A and all the models that could be derived from it by removing fixed-effect variables (null model included) were compared using Akaike information criterion corrected for small samples (AICc). In a second step, the models considered were fitted to the entire habitat selection dataset, and derived from the full model 'B':

$$Y \sim woody\ debris\ cover * hole * season + (1|id) + (1|site)$$

where 'season' is a binary variable taking value 0 for the breeding season and 1 for the post-breeding season. As previously, full model B and all the models that could be derived from it by removing fixed effects were compared using AICc. In addition, deviance test was sometimes used to compare nested models.

Finally, we described the distances at which individuals moved away from aquatic sites. During the breeding season, we focused on the distance between each terrestrial shelter and the aquatic site most recently used by the same individual to assess whether individuals remained close to, or moved away from, the aquatic sites potentially used for reproduction. During the post-breeding season, we focused on the distances between each individual's terrestrial shelters and the aquatic site in which it was captured at the beginning of the season. For the eight individuals tracked during both seasons, the recapture site was an aquatic site used during the breeding season, and we assumed that the same applied to two other individuals captured for the first time in the post-breeding season. We chose this distance in order to evaluate how far individuals moved between their aquatic sites used in the breeding period and their potential autumn/winter refuges.

All the analyses were performed using R® (R Core Team, 2023), with RStudio (v.2025.09.02). Package "lme4" (Bates et al., 2015) was used for the GLMMs, and package "MuMIn" (Bartoń, 2024) for model comparison based upon AICc.

RESULTS

A total of 31 yellow-bellied toads were monitored: 29 during the breeding season, and 10 during the post-breeding season. Eight of the 10 individuals tracked during the post-breeding season had previously been monitored during one of the two sessions of the breeding season (Table 2). The number of locations per individual ranged from 6 to 51 in the breeding season (mean: 30.8) and from 16 to 41 in the post-breeding season (mean: 29.7). Differences in monitoring duration resulted from some individuals losing their transmitters or from the intentional removal of the equipment before the end of the tracking period. Transmitters were intentionally removed in cases of excessive weight loss (>15%) or minor injuries (observed in two individuals). Upon recapture, all affected individuals were found to be in good health and fully healed.

Terrestrial shelter use

Proportion of locations in shelters varied greatly between individuals (breeding season: 0–50.0%; post-breeding: 0–75.0%), and its overall value (individuals combined) was higher in post-breeding than during the breeding season (breeding season: 3.1%; post-breeding: 25.6%; χ^2 = 141.08, $P_{perm.}$ = 0.0086). Similarly, the average number of locations in the same shelter varied greatly among individuals observed to rest in shelters (breeding season: 1–3; post-breeding: 1–18), and its overall value was higher in post-breeding than during the breeding season (breeding season: 1.333; post-breeding: 3.304; difference: 1.971, $P_{perm.}$ = 0.0435).

Selection of terrestrial shelters

Whatever the season, the GLMM including ‘woody debris cover’ and ‘holes’ as only fixed-effect variables was both the best GLMM derived from full model ‘A’ and the most parsimonious model among those with ΔAICc ≤ 2 (Table 3). However, among the GLMMs fitted to the entire dataset and derived from full model ‘B’, the best model included not only 'debris cover' and 'hole', but also 'season' and the interaction between 'season' and 'hole' (Table 4). No alternative model had a ΔAICc ≤ 2 in this case (Table 3), and the effect of the season was significant (deviance test; $\chi^2_2 = 11.607$, P = 0.003).

Indeed, while holes were preferentially used as shelters in both seasons, resting places were sometimes found outside holes in the breeding season but never in post-breeding. Moreover, regardless of the season, yellow-bellied toads preferred to shelter where woody debris cover was higher than 50% (Fig. 2).

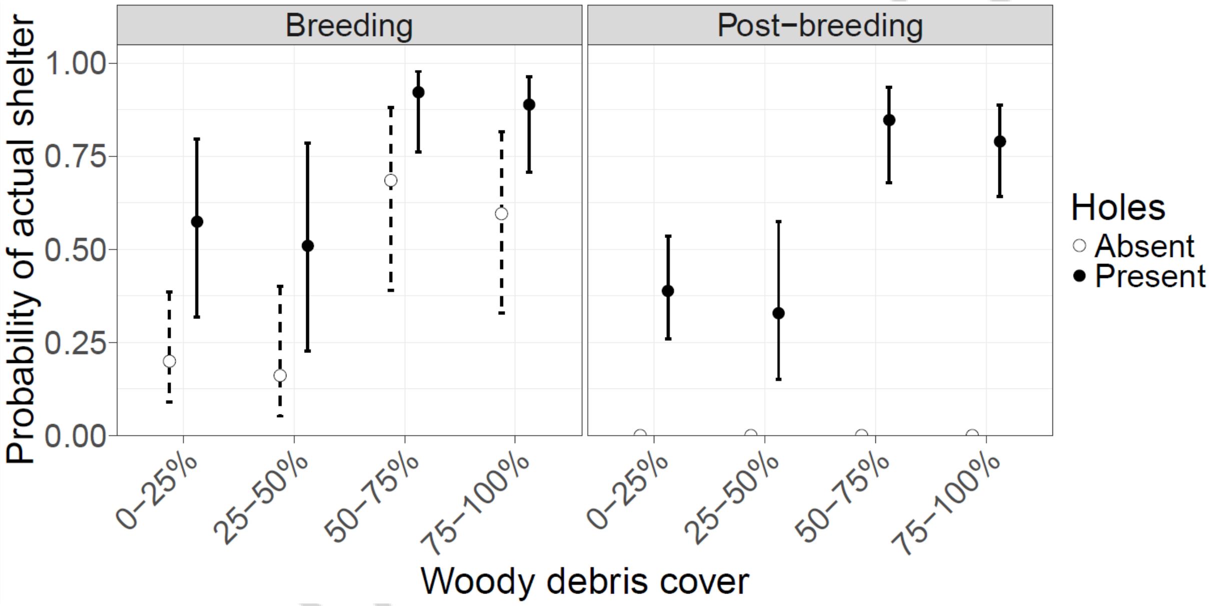

Fig. 2. Estimated probability (± 95% CI) that a location is a shelter used by a yellow-bellied toad (rather than a random location) as a function of hole presence/absence and proportion of the ground covered by woody debris at that location. Estimates are those obtained using the model with the lowest AICc value in Table 4. In post-breeding season, the probability of actual shelter is 0 for locations without holes, and the model does not provide any reliable estimate for CI in this case.

Distances of terrestrial shelters to water

During the breeding season, distance between a shelter and the water body most recently used by the same individual ranged from 0.1 to 214 m (median: 6 m; mean: 50.1 m; n = 29).

The range was the same for the maximum distance recorded per individual (Table 5), with a median of 9 m and a mean of 43.8 m (n = 10).

During the post-breeding period, the maximum distance between an individual's shelter and the first water body where it was captured ranged from 0.3 to 285 m (Table 6) with a median of 9 m and a mean of 50.9 m (n = 9).

DISCUSSION

This study is the first to investigate the use and selection of terrestrial shelters by Yellow-bellied Toads. Radio telemetry proved valuable for this purpose, despite constraints related to the species' small body size, which required the use of very lightweight transmitters with limited battery life. These limitations were considered in the study design and inevitably influenced the quantity of data collected. However, they are unlikely to have affected data quality, and our results provide a robust basis for integrating terrestrial habitats into conservation considerations for this species.

Terrestrial shelters use

Most individuals used terrestrial shelters only sporadically during the breeding season, and more frequently during the post-breeding period. Such shelters may serve several functions. In some species, they provide refuge from adverse environmental conditions during the breeding season, particularly during drought events (Daversa et al., 2012; Scheffers et al., 2014; Evans et al., 2020; Forti et al., 2022; Pujol-Buxó and Montori, 2025). In these situations, shelters may be used for extended periods; however, this was not observed in our study, as shelters were used on average only once or twice during the breeding season (up to four times). This pattern instead suggests occasional use as resting sites, located near breeding areas or used during movements. During the post-breeding period, the more frequent use of terrestrial shelters may be associated with the search for overwintering sites, either as temporary refuges during movements or as more permanent shelters in preparation for winter, as reported in other amphibian species (Schabetsberger et al., 2004; Tong et al., 2023).

Terrestrial shelters selection

Our results suggest that individuals preferentially selected shelters with characteristics likely to maintain adequate moisture levels with stable temperature (Cohen and Alford, 1996; Burrow and Maerz, 2022; Pujol-Buxó and Montori, 2025), and provide opportunities for burrowing, regardless of the season. This pattern likely reduces desiccation risk, a well-documented constraint in amphibians (Tracy, 1976; Shoemaker et al., 1992; Schwarzkopf and Alford, 1996). Similar preferences have been reported in other species, in which terrestrial habitat selection is strongly influenced by moisture-related features and the availability of underground refuges. For example, Cohen and Alford (1996) showed that *Rhinella marina* used artificial microhabitats with low insolation exposure and reduced air movement, which favors the maintenance of soil moisture. Another study highlighted that *Lithobates chiricahuensis* selected terrestrial habitats with low-lying cover and moist substrate to reduce the risk of desiccation (Hinderer et al., 2021). Richter et al. (2001) reported the selection of underground refuges, such as small-mammal burrows or stump holes, by *Lithobates sevosus* after the breeding period.

In our study, individuals were found in a variety of microhabitats, including piles of twigs, humus crevices, decaying stumps, accumulations of bark, and likely rodent burrows (underground detection). This is consistent with a previous exploratory study that identified cracks and rodent burrows as potential overwintering sites (Pichenot, 2008). During autumn, the presence of cavities appears to be a key factor in shelter selection, possibly because such structures provide access to underground refuges that can be used over extended periods, potentially including part of the winter season.

Distance of terrestrial shelters to water

During the breeding season, distances between terrestrial shelters and aquatic sites ranged from a few meters to several hundred meters, likely reflecting differences in their function. Some shelters were probably used as resting sites in close proximity to breeding areas, whereas others served as refuges during movements. Di Cerbo (2001) and Winkler et al. (2025) observed that the presence and abundance of the species were associated with the availability of terrestrial mineral refuges, such as crevices or piles of stones, near aquatic sites. Our findings clearly confirm that terrestrial shelters are necessary for individuals near aquatic sites during the breeding season, and further suggest that this is also the case throughout their entire range during their movements.

After breeding, individuals leave aquatic sites in search of overwintering areas (Hartel, 2008; Pichenot, 2008). The terrestrial shelters used during this period may therefore correspond either to temporary refuges during movements or to sites eventually used for overwintering. Although a few individuals were last located in terrestrial shelters, it cannot be determined whether these sites were ultimately used during winter. Nevertheless, marked variability was observed in the distances traveled from the aquatic capture site. Some individuals selected shelters relatively close to aquatic sites, whereas others moved much farther away. This pattern may reflect interindividual differences in behavior. Some toads may act as dispersers, taking advantage of favorable conditions to initiate movements as early as autumn, as described in Beshkov and Jameson (1980), while others may be more sedentary, selecting shelters close to the aquatic sites to which they show site fidelity (Barandun and Reyer, 1998). Alternatively, this pattern may result from local habitat availability, with some individuals forced to travel greater distances due to a lack of suitable terrestrial shelters near certain aquatic sites. Future studies should examine whether individuals return to the same aquatic sites in the following year, bearing in mind that some may be non-reproductive and therefore undetectable at breeding sites (Cayuela et al., 2014). In any case, the distances reported here should therefore be considered as conservative estimates of movement capacity in this context, as (i) tracking did not cover the entire post-breeding period due to the limited battery life of transmitters, and (ii) only adults were tracked, as individuals of other age classes were too small to carry the equipment. The distances travelled by juveniles may be greater, as this age group has been observed to disperse the most (Płytycz and Bigaj, 1984; Gollmann et al., 2000).

CONCLUSION

From a conservation perspective in forest habitats, our results suggest that retaining woody debris on the ground (e.g., fallen trees, bark, piles of twigs, stumps) is likely to increase the availability of suitable refuges for the species, both in the immediate vicinity of aquatic sites and within a radius of at least 300 m. More generally, the removal of woody debris should be minimized wherever possible across the area occupied by a population, particularly during winter. Such practices would likely benefit not only this species but also other amphibians, including both urodeles (LeGros et al., 2014) and anurans (Indermaur and Schmidt, 2011; Pabijan et al., 2023), as well as a range of associated taxa (Paillet et al., 2010). Further research is needed to improve our understanding of terrestrial shelter use. In particular, tracking individuals throughout the entire winter season and over multiple consecutive years would provide valuable insights, once further miniaturization of tracking devices allows for such long-term monitoring. This would help determine whether individuals exhibit site fidelity to overwintering sites, as reported in other species (Cohen and Alford, 1996), and would support more targeted management of woody debris. In some cases, this may involve deliberately leaving cut wood on the ground in specific areas where the species is present.

AUTHORIZATIONS

Permission for amphibian capture and manipulation was granted by the Direction Régionale de l'Environnement, de l'Aménagement et du Logement (DREAL) of the Grand Est region, Prefectural Order No. 2023-DREAL-EBP-0064. All manipulation procedures were carried out after completing training in wildlife experimentation ("Use of non-captive wild animals for scientific purposes"), with a specific module on amphibians, provided by the Ministry of Agriculture under no. R-75-MNHN-F1-15 with the National Museum of Natural History (MNHN), the French Biodiversity Agency (OFB), and the National Centre for Scientific Research (CNRS). The experiments were conducted in accordance with Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes. The institution hosting the study holds authorization as user establishment for the use of animals for scientific purposes (B-08-075-1) and is affiliated with the Reims Champagne-Ardenne Animal Experimentation Ethics Committee.

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TABLES

Table 1. Fixed-effect variables used to analyze habitat selection by Yellow-bellied toads during each season. These variables correspond to characteristics recorded within a 1-meter diameter centered on each shelter and each random location.

Variable	Description
water	Presence of water: 0 or 1
holes	Presence of holes: 0 or 1
woody debris cover	Percetage of woody debris cover: [0-25%], [25-50%], [50-75%] or [75-100%]
shrub cover	Percentage of hidden sky by shrub: [0-25%], [25-75%], [75-100%]
tree cover	Percentage of hidden sky by trees: [0-25%], [25-75%], [75-100%]
herbs	Presence of herbaceous substrate : 0 or 1
slope	Presence of sloping ground: 0 or 1

Table 2. Number of different individuals of yellow-bellied toads tracked, the total of their locations and the number of locations in terrestrial shelters TS).

Period	Number of individuals		Number of locations	
	Females	Males	Total	TS
Breeding	15	14	924	29
Post-breeding	6	4	297	76

Table 3. Fixed part of the GLMMs (family: binomial; link: logit) that derived from full model A and best fitted the habitat selection data of yellow-bellied toads for each season. Models are listed down to the first one with a ΔAICc > 2 (in italics).

Models	df	AICc	ΔAICc	weight
Breeding season				
holes + woody debris cover	7	73.8	0.00	0.212
holes + woody debris cover + water	8	75.5	1.73	0.089
woody debris cover + water	*7*	*76.0*	*2.28*	*0.068*
Post-breeding season				
holes + woody debris cover	7	160.3	0.00	0.110
holes + woody debris cover + slope	8	160.6	0.37	0.092
holes + woody debris cover + shrub cover	8	160.9	0.66	0.080
holes + woody debris cover + herbs	8	161.9	1.65	0.048
holes + woody debris cover + slope + shrub cover	9	161.9	1.69	0.047
holes + woody debris cover + shrub cover + herbs	9	162.0	1.76	0.046
holes + woody debris cover + water	8	162.2	1.99	0.041
holes + woody debris cover + slope + shrub cover + herbs	*10*	*162.3*	*2.09*	*0.039*

Table 4. Fixed part of GLMMs (family: binomial; link: logit) derived from full model B and fitted to the two seasons' habitat selection data of yellow-bellied toads. The two best models are presented, as well as a simpler model including only woody debris cover and hole presence as additive fixed-effect variables. Models with ΔAICc > 2 are in italics.

Models	df	AICc	ΔAICc	weight
holes + woody debris cover + season + holes:season	9	223.2	0.00	0.169
holes + woody debris cover + season	*8*	*226.1*	*2.86*	*0.040*
...				
holes + woody debris cover	*7*	*230.5*	*7.26*	*0.019*

Table 5. Maximum distance between TS and the aquatic site most recently used by each individual monitored during the breeding season. *individual for whom the farthest shelter corresponds to the last location.

Individual	Sex	Max distance to last aquatic site	Number of location in shelters
Sucrine	F	0.1	3
Sombre*	F	0.5	1
Salvo	M	2.0	1
Savonnette	F	2.0	1
Salade	F	5.0	1
Semoule	F	13.0	3
Sommeil	M	20.0	2
Sirius	M	95.0	5
Surprise*	F	100.0	2
Speedy	M	200.0	10

Table 6. Maximum distance between TS and the initial aquatic site for each individual monitored during the post-breeding season. *individual for whom the farthest shelter corresponds to the last location.

Individual	Sex	Max distance to first aquatic site	Tracking duration (days)
Sariette	F	0.3	8
Sommeil	M	1.5	12
Snoopy*	M	2.0	17.5
Surprise	F	4.0	12
Sushi	F	9.0	14
Sirene*	F	41.0	20.5
Solstice	F	45.0	16.5
Salto	M	70.0	11
Speculos*	M	285.0	20

FIGURE CAPTIONS

Fig. 1. Study area (black square) in the Meuse department (grey), France.

Fig. 2. Estimated probability (± 95% CI) that a location is a shelter used by a yellow-bellied toad (rather than a random location) as a function of hole presence/absence and proportion of the ground covered by woody debris at that location. Estimates are those obtained using the model with the lowest AICc value in Table 4. In post-breeding season, the probability of actual shelter is 0 for locations without holes, and the model does not provide any reliable estimate for CI in this case.