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New data on the nesting sites selection and breeding success of three bird species in the riparian vegetation of Northwest African rivers

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Abstract Many avian species partition feeding and breeding resources to avoid competition for nesting and food elements. This competition frequently leads to the segregation of space and time use among cohabiting species. The breeding requirements of coexisting species and drivers of segregation are poorly understood in passerine birds. In this study, we monitored nesting habitats, nest placement, and breeding success among two passerine birds, *Hippolais polyglotta* and *Turdus merula*, and the Columbidae species *Streptopelia turtur arenicola*, in rivers of the upper Moulouya (Morocco) Mountains to examine the levels of habitat partitioning, success rates, and governing factors during the breeding season. We recorded the nests, nesting sites, nest placements, and success rates of the studied species along three rivers during 2017 and 2019. Our results revealed important breeding activity in the studied birds, with 420 nests of *H. polyglotta* and 88 nests of *T. merula*, compared to 99 nests of *S. t. arenicola*. Nest niches were segregated between passerines and Columbidae and within passerines. Nesting sites were segregated along sections of rivers except for nests of *H. polyglotta*, which were shared between upstream and intermediate zones. Nest substrates were partially segregated among the three species; nests of *H. polyglotta* and *S. t. arenicola* were commonly constructed on *Crataegus monogyna* and *Rosa canina* substrates, while nests of *T. merula* were on Salix sp. Similarly, vertical placements of nests were segregated among birds. Breeding success rates differed among birds (94.44% in *T. merula*, 87.88% in *H. polyglotta*, and 55.56% in *S. t. arenicola*) due to human and natural factors. Finally, this study confirmed the first breeding case of *H. polyglotta* on the southern slope of the Mediterranean and provided new insight into nest niches in cohabiting passerines and Columbidae species cobred in riparian vegetation in Morocco and the entire region of North Africa. However, future investigations are required to understand the main reasons behind the selection of nesting habitats for passerine species, particularly in farmlands.

Keywords: breeding sites, nest-niche partitioning, breeding success, passerines and columbidae, riparian vegetation

1. Introduction

Knowledge of niche ecology, including the selection of nesting sites and their effect on bird breeding success, has recently become crucial to understanding their productivity (Han et al. 2019; Laikun et al. 2021; Squalli et al. 2022a). This interest was stimulated in part by the decline in breeding habitats brought about by human activities (i.e. expansion of farms and deforestation), and climate change that destroy entire ecosystems such as lakes, rivers, and forests (Fan and Shibata 2015; Wauchope et al. 2017; Traba and Morales 2019). Currently, during the breeding season, nesting habitat requirements are given more consideration (Begehold et al. 2015; Tapia et al. 2018). Moreover, bird productivity and the recovery of fragile species depend greatly on breeding habitats (Assandri et al. 2017; Kettel et al. 2018).

Although different bird species choose different breeding sites, the mechanisms governing habitat utilization are still poorly understood (Dinkins et al. 2014; Mainwaring 2015; Squalli et al. 2021). Standard nest-niche hypotheses claim that avian species select nesting sites in well-safe environments, far from competitors and predators, and close to foraging resources (Bonaparte and Cockle 2017; Han et al. 2019; Mansouri et al. 2022a). For example, the fragile Turtle dove (*Streptopelia turtur arenicola*) chooses breeding locations near rivers and cereal fields where it feeds and away from competitors and predators (Mansouri

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et al. 2019; Squalli et al. 2021; Squalli et al. 2022c). This approach enables the bird to guarantee a higher rate of successful reproduction by safeguarding the fledgling and providing nourishment for them (Squalli et al. 2022c). However, these features have not been well investigated in other avian groups in arid areas characterized by a scarcity of foraging and breeding resources.

In Morocco, avian species are widely distributed from the Mediterranean coasts to the southern borders of Mauritania (Bergier et al. 2022). The Moroccan avifauna is composed of nearly 588 species of migratory, resident, and accidental species (Bergier et al. 2022). They have been investigated in forests (Mounir et al. 2022), wetlands (Cherkaoui et al. 2018), farmlands (Hanane 2016), and urban ecosystems (Douini et al. 2022). For example, Turtle doves have been studied in farmlands (Mansouri et al. 2020; Mounir et al. 2023), forests (Hanane 2018), and per-urban landscapes (Squalli et al. 2022d). However, these studies focused on breeding biology, ecology, and geographical distribution, while nest-niche investigations are rare and limited. For example, Mansouri et al. (Mansouri et al. 2022a) studied the coexistence of five Columbidae strains, while Squalli et al. (Squalli et al. 2021; Squalli et al. 2022c) investigated the coexistence of Columbidae strains and predatory birds. All these studies were limited to columbiforms, which are very poor in terms of the diversity of avian species in Morocco.

Passerines are the most abundant avian group in Morocco (Mansouri et al. 2021c; Mounir et al. 2022; Achiban et al. 2022; Squalli et al. 2022a); they are encountered on Atlantic coasts from the Mauritanian borders in the South to the Mediterranean coasts in the North (Hama et al. 2013; Cherkaoui et al. 2015; Cherkaoui et al. 2018; Arizaga et al. 2020). They are well studied in farmlands, forests, and urban areas, while studies on these birds are less (Squalli et al. 2022a)common in riparian ecosystems . To better understand the ecological nesting niches of the little passerines in this region, further research on the selection of nesting locations, placement, and utilization of nesting resources is recommended. Similarly, the expansion of an arid climate in 75% of the Moroccan territory is suggested to push nesting sites of these birds toward more humid areas such as river ecosystems. Therefore, climate drivers need to be included in such investigations.

In this paper, we aim to investigate the nest niches of three species, namely, the two passerines blackbird (*Turdus merula*) and the melodious warbler (*Hippolais polyglotta*), and the North African subspecies of the European turtle dove (*Streptopelia turtur arenicola*) within Columbiformes in the Upper Moulouya region (central Morocco). In detail, we aimed to investigate the distribution of nesting sites along river sections and the vertical segregation of nest placement among cohabiting birds. Similarly, we compared breeding success and evaluated its predictors and influencing factors. We used *Streptopelia turtur arenicola* as a reference species because it is the most studied species in Morocco and North Africa concerning nesting strategies (Mansouri et al. 2020; Squalli et al. 2022d), nest niches (Squalli et al. 2021; Squalli et al. 2022c), and breeding success (Mansouri et al. 2021b). Therefore, comparisons with this threatened species are suggested to clarify the nest niches of the other two passerines, which are considered less investigated.

2. Materials and Methods

2.1. Study area

Field visits were made in the upper Moulouya plain, which is located at the foot of Jbel Ayachi in the Eastern High Atlas and at the junction with the chains of the Middle Atlas. The study zone is situated at an altitude of 1300–1700 m above sea level and is characterized by semiarid and arid climates with cold winters. The average annual temperature in upper Moulouya is 14.1 °C, and the average rainfall is 294 mm per year.

The hydrographic network of upper Moulouya is important, principally in the mountains, and weak on the plains. The Moulouya wadi is the main collector of the basin; along its route, it receives a very large number of tributaries, including the Ansegmir wadi and the Sidi Ayad wadi (Ahamrouni 1996). These hydrologic systems offer water for agriculture dominated by fruit trees (apples, olives, apricots, and peaches), as well as cereals (wheat and barley), which cover nearly 804.354 ha. The study plain is also dominated by forests (185.004 ha) and steppes (280.000 ha).

Three study rivers, Ansegmir, Tablkhirt, and Moulouya, were selected and monitored from 2017 to 2019 (Figure 1). The rivers were divided into three sections: upstream, intermediate, and downstream. The upstream area was delimited from the origin of the river to the first farmlands on both sides. The intermediate zones were delimited between the first agricultural lands upstream and the last farmlands in the direction of the dams. The downstream area was delimited between the last farmlands and the dams. This division was based on the presence of human activities, principally farmlands and geomorphologic features (i.e., gorges upstream, flat terrains in the intermediate zone, and lowlands and dams downstream).

2.2. Nest-niche data

To collect avian data, field visits were made monthly between December and September during the 2017 and 2019 breeding seasons. A transect method was used along the river sections. The length of each transect was nearly 6 km. The search for nests was performed in riparian vegetation on both sides of the river streams, with a radius of 30 m. During each visit, we documented the number of nests, nesting sites (following river sections), nest substrates (nesting tree species), and position of nests in each substrate type. In addition, we measured the heights of both nests and substrate types (m) and noted the morphology of nests by counting their diameters and depths (cm) to differentiate among the studied bird species. Measurements of nest placement and morphology were performed with a digital ruler at the end of the breeding season to avoid disturbing the broods. Before measurement, each nest was assigned a specific identifier, after which the long and short diameters (long and small axes of nests) and nest depth were measured with a digital ruler. The length of the monitored ecosystems was as follows: 26 km in Ansegmir, 10 km in Tablkhirt, and 15 km in Moulouya.

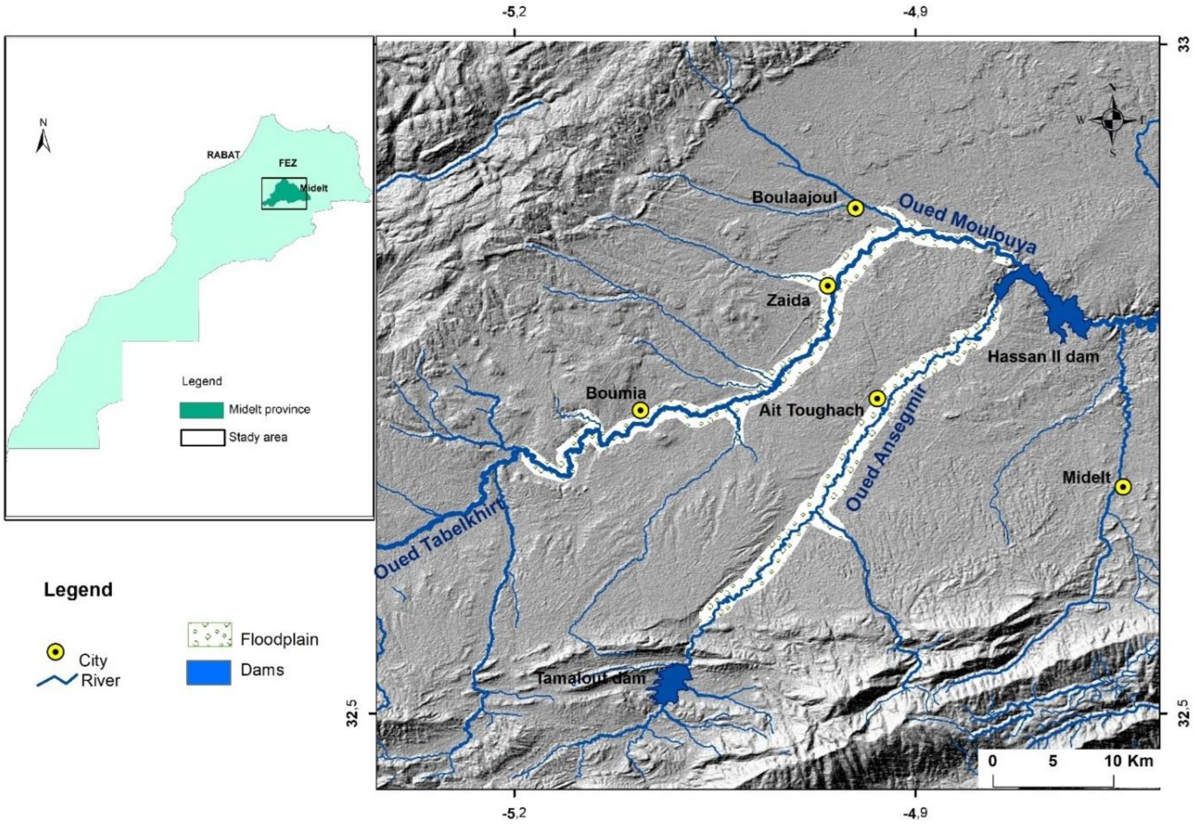

Figure 1 Locations of the study sites from 2017 to 2019.

2.3. Rates of breeding success

Nests were monitored from their construction to the fledging or loss of clutches. The breeding success rate was calculated as the number of successful nests per constructed nest. A nest was considered successful when at least one brood flew. Similarly, we noted the failure factors for each species (predation, mortality, disturbance, etc.) during the nesting, laying, and incubation of chicks. This approach was used by Mansouri et al. (Mansouri et al. 2021b) and Squalli et al. (Squalli et al. 2022d) to evaluate the breeding success and failure factors during each breeding phase, which is impossible with methods that use the number of fledglings for nests. In parallel, we documented human and natural factors suggested to influence the breeding success of the studied species. We noted distances separating nests from the nearest human-made landscapes (farmlands, infrastructure, buildings, etc.), roads, and river streams (suggested to offer water in this arid area). Furthermore, to estimate these distances, nests were recorded in a mobile application (Geotracker, GPS tracker), and then the files (KMZ form) were exported into Google Earth Pro. The distances were estimated between nests and fixed variables using the measurement option of distance (we fixed the nest as a point and the nearest side of a human-made habitat as a second point; then, the distance could be extracted automatically) (Hanane 2018; Mansouri et al. 2022a).

2.4. Statistics

Monitored variables were tested for normality using the Kolmogorov–Smirnov test. We compared the breeding populations (number of nests) of the three bird species (n=3) via one-way ANOVA, and we considered two breeding seasons and three nesting sites (rivers) for each species (n=6). Similarly, nest placement (height of nests and substrate types), nest morphology (long diameter, short diameter, and cup depth), and breeding success (successful nests/total constructed nests) were compared via one-way ANOVA. For all nesting and breeding parameters, we considered three rivers and two breeding seasons. The results were considered significant at $P<0.05$ and are presented as the sample size and mean ± SD.

To evaluate the levels of habitat partitioning, nests (N= 314 nests) of breeding birds (N= 3) were considered response variables (response= 0 absence of nest at the site, response=1, at least one nest of a bird was recorded at the site), while potential nesting sites in river sections (n= 3 (upstream, intermediate zone, and downstream)) were measured as descriptive variables and were analyzed via detrended correspondence analysis (DCA) (only axes with eigenvalues >1.0 were selected). The principal factors that affect the nests of birds were analyzed via principal component analysis (PCA). Similarly, we used the dimensions (diameters and cup depth) and vertical placements (nest and substrate height) of nests to determine the areal segregation of nest niches among the studied species via 3D principal component analysis (3D PCA). Furthermore, the impacted nests of the studied birds were considered dependent variables, while potential factors related to predation and desertion during the construction, laying, and fledging stages were considered independent variables. Only components with eigenvalues >1.0 were selected and are presented as percentages of variance. To evaluate the potential habitat features suggested to influence the breeding success of the monitored birds, we used multiple regression analysis. The success of nests was considered a dependent variable, while the distance to the nearest human activity (D.H.A.), to the nearest coexisting nest of the same species (D.N.C.N.), to the nearest water stream (D.N.W.), and to the nearest road (D.N.R.) were considered independent variables. All analyses were performed using Statgraphics Centurion XVI.

3. Results

3.1. Nesting activity

The results of nesting activities in the rivers of the upper Moulouya River during the 2017–2019 breeding season are presented in Figure 2. In total, 420 nests of the studied species were recorded in the riparian vegetation of the Moulouya tributary rivers. Furthermore, nests of *H. polyglotta* was the most abundant (233 nests), followed by *S.t. arenicola* in the second rank (99 nests), and *T. merula,* with 88 nests (Figure 2-A). The number of recorded nests varied among the monitored ecosystems (Figure 2-B). In Ait Ayach, the number of recorded nests was estimated to be 187, and the nests were dominated by *H. polyglotta* (144 nests), followed by *T. merula* (34 nests), while only 9 nests were recorded for *S.t. arenicola.* Furthermore, 143 nests were documented in Boumia: 55 nests in *H. polyglotta*, 51 nests in *S.t. arenicola*, and 37 nests in *T. merula*. In Boulbzouz, only 89 nests were recorded: 38 nests of *S.t. arenicola*, 34 nests of *H. polyglotta*, and only 17 nests of *T. merula*.

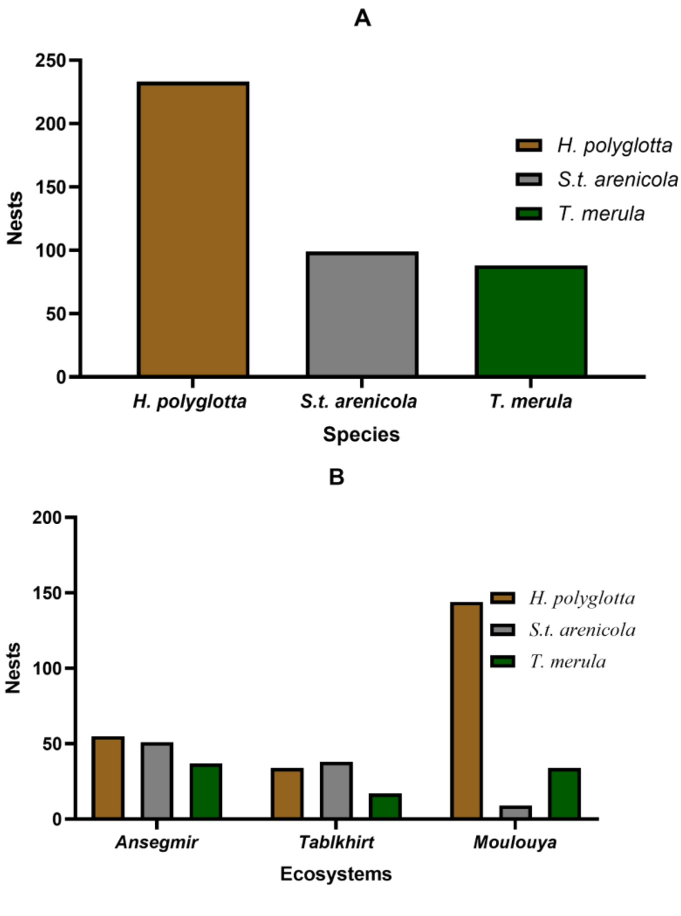

Figure 2 Nesting activity of the three breeding species (A) in the Moulouya tributary rivers (B)

3.2. Distribution of nests and support trees

The longitudinal distribution of nests following river segments is presented in Figure 3. The nests of all studied bird species were recorded from upstream to downstream. However, nests of *S. t. arenicola* were concentrated in the intermediate zones and downstream areas of the monitored rivers. In contrast, nests of *T. merula* were principally built in the upstream zones of rivers, while nests of *H. polyglotta* were shared between the upstream and intermediate zones of rivers.

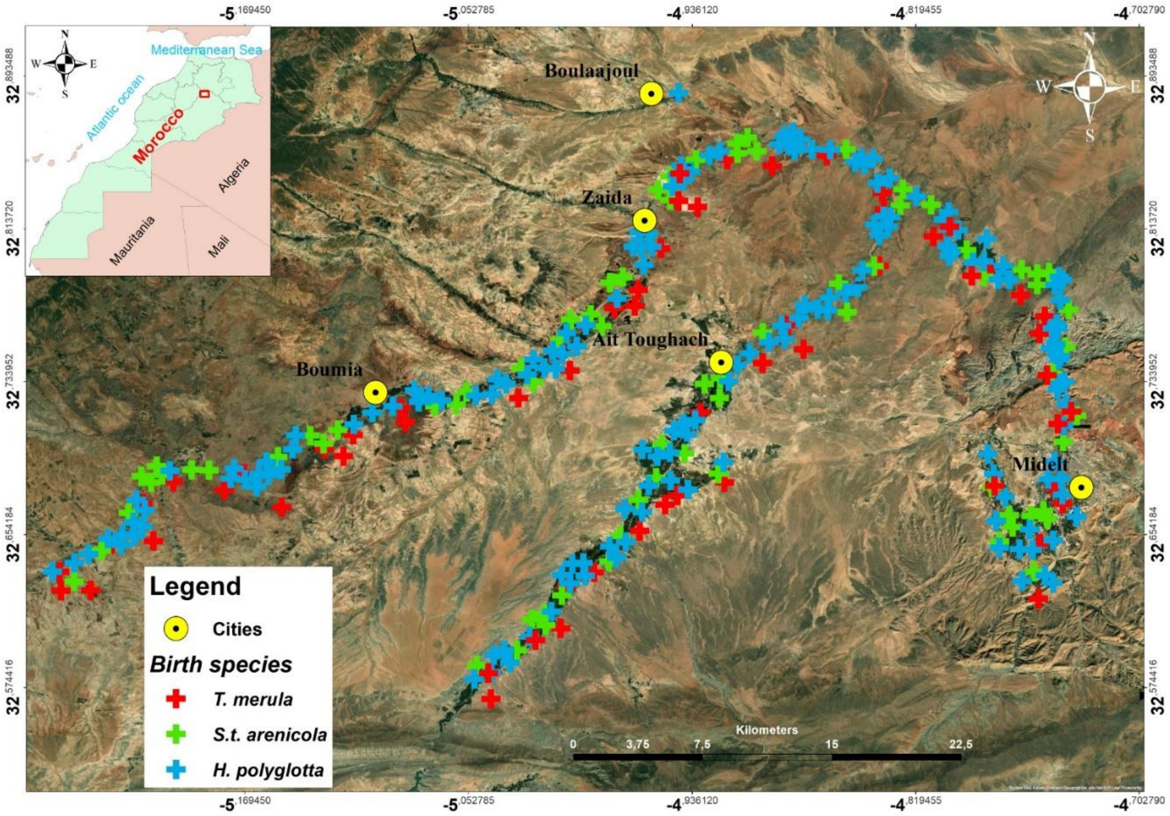

Figure 3 Distribution of bird nests in the upper Moulouya.

Cohabiting bird species use different nesting trees along monitored rivers (Figure 4). Nests of both *H. polyglotta* and *S. t. arenicola* were commonly constructed on hawthorn (*Crataegus monogyna*) and wild rose (*Rosa canina*). In contrast, nests of *T. merula* were found principally on trees of *Salix* sp. and partially on *Poplar* sp. In detail, *H. polyglotta* built its nests principally on *Salix* sp. (99 nests), *Rosa canina* (48 nests), *Poplar* sp. and *Crataegus monogyna* (27 nests) (Table 1). Only three nests of *H. polyglotta* were recorded on *Rubus fruticosus,* and one was recorded on *Plum* sp. Nests of *S.t. arenicola* were principally on *Rosa canina,* with 62 nests, and *Crataegus monogyna* had 27 nests. In contrast, only three nests of *S.t. arenicola* were recorded on both *Tamarix* sp. and *Salix* sp., and one nest was recorded on four substrates: *Poplar* sp., *Plum* sp., *Rubus fruticosus,* and *Cydonia oblonga.* The nests of *T. merula* were concentrated on *Rosa canina* (56 nests), *Salix* sp. (10 nests), and *Poplar* sp. (8 nests). Only five nests were recorded on *Crataegus monogyna*, four on *Tamarix* sp., two on both *Cydonia oblonga* and *Plum* sp., and one on *Rubus fruticosus.*

3.3. Nest placement and morphology

The placement of nests on nesting trees and the nest morphology of the studied species are summarized in Table 2. Nests of both passerines *H. polyglotta* and *T. merula* were taller than those of the Columbidae *S. t. arenicola*. In contrast, vertical placements were inversed between the two groups*. The nests of S. t. arenicola* were placed at relatively high elevations, while the nests of *T. merula* and *H. polyglotta* were placed at relatively low elevations. Similarly, nest morphology differed among the studied species. Nests of *H. polyglotta* and *T. merula* were characterized by short diameters (long and short diameters) compared to *S.t. arenicola, which is* characterized by large dimensions. In contrast, the cup depth of nests was significantly greater for *H. polyglotta* and *T. merula* than for *S.t. arenicola.* The segregation of nest niches among the studied birds was confirmed via 3D component analysis (Figure 5). The areal delimitation of nest niches was close between the passerines *T. merula and* H. *polyglotta.* In contrast, the nest niche of *Columbidae S. t. arenicola* was segregated from passerines.

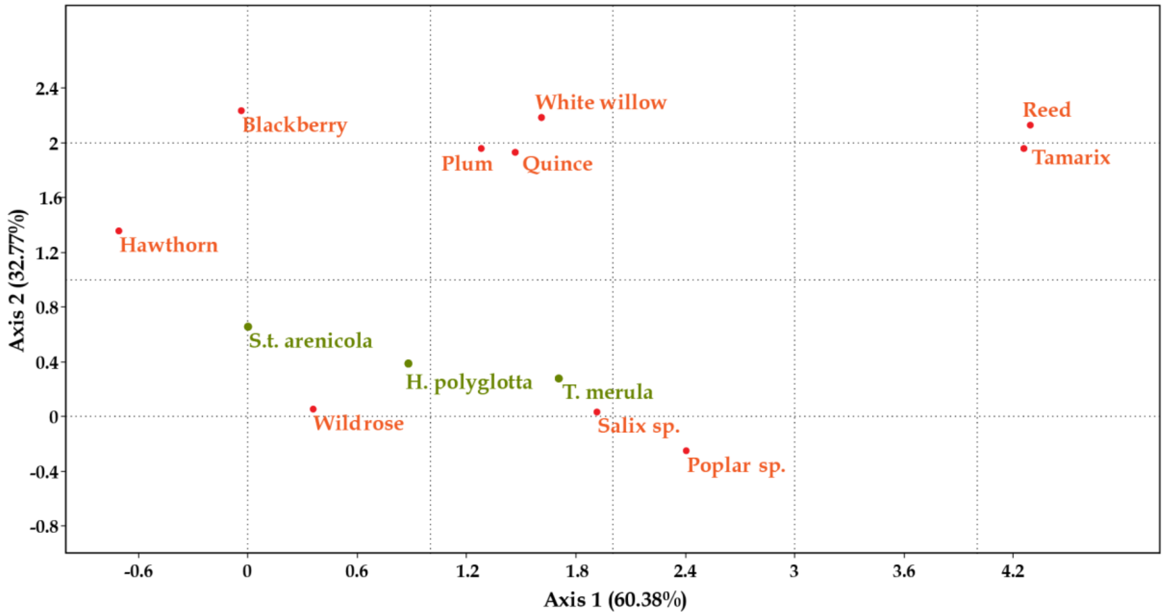

Figure 4 Affinity of breeding species for nesting trees in the Moulouya tributary rivers.

Table 1 Nesting substrates used by breeding species in the Moulouya tributary rivers.

	H. polyglotta	*S.t. arenicola*	*T. merula*
Rosa canina	48	62	56
Crataegus monogyna	27	27	5
Salix sp	99	3	10
Poplar sp	33	1	8
Plum sp	1	1	2
Rubus fruticosus	3	1	1
Tamarix sp	22	3	4
Cydonia oblonga	0	1	2

Table 2 Placement and morphology of nests of the studied birds.

Parameters	*S. t. arenicola*	*T. merula*	*H. polyglotta*	F	*P Value*
Height of nesting Substrate (m)	5.21±0.72	5.86±1.33	5.86±1.33	9.167	<0.001
Nest height (m)	2.06±0.15	1.96±0.16	1.96±0.16	23.456	<0.001
Nest long diameter (cm)	11.64±0.47	9.22±0.20	9.19±0.20	50.224	<0.001
Nest short diameter (cm)	9.08±0.42	6.76±0.16	6.74±0.15	58.211	<0.001
Nest cup depth (cm)	6.51±0.38	8.32±0.41	8.23±0.40	26.364	<0.001

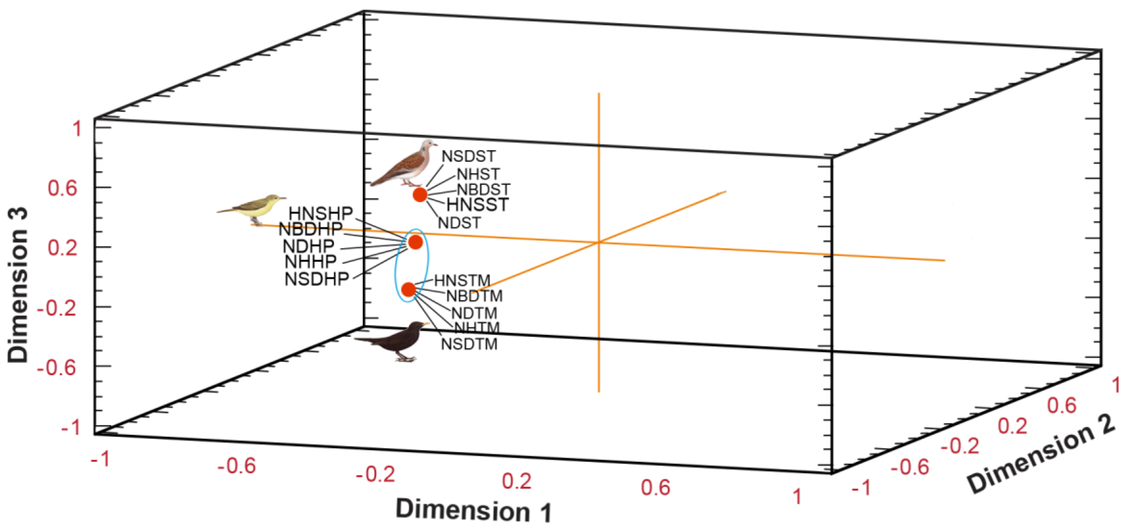

Figure 5 Segregation of the nests of *H. polyglotta, T. merula,* and *S.t. arenicola* in the Upper Moulouya River according to PCA (3D plot).

3.4. Productivity and failure factors

The rates of breeding success of the studied species are presented in Table 3. Among the 88 recorded nests of T. merula, 83 fledged (94.44%), while only five failed (5.56%). In *H. polyglotta,* among the 233 recorded nests, 205 produced fledging (87.88%), while only 28 nests failed (12.12%). Among the 99 recorded nests of *S. t. arenicola,* 55 produced fledging (55.56%), and 44 failed (44.44%). On the other hand, the nests of the studied species were affected by various factors (Figure 6). During the laying stage, 36.36% of nests failed, while 20.45% of nests failed during the incubation of chicks. Nests of *S. t. arenicola* were impacted by predation. In *H. polyglotta,* nests were principally impacted by the destruction that affected 56.25% of the nests. In contrast, nests of *T. merula* were spared from all the cited factors (only two nests were lost).

Table 3 Productivity rates of passerines in riparian vegetation of the upper Moulouya.

Parameters	*S. t. Arenicola*	*T. merula*	*H. polyglotta*
Total nests	99	88	233
Successful nests	55	83	205
Rate of success (%)	55.56*	94.44***	87.88**
Failed nests	44	5	28
Rate of failure (%)	44.44***	5.56*	12.12**

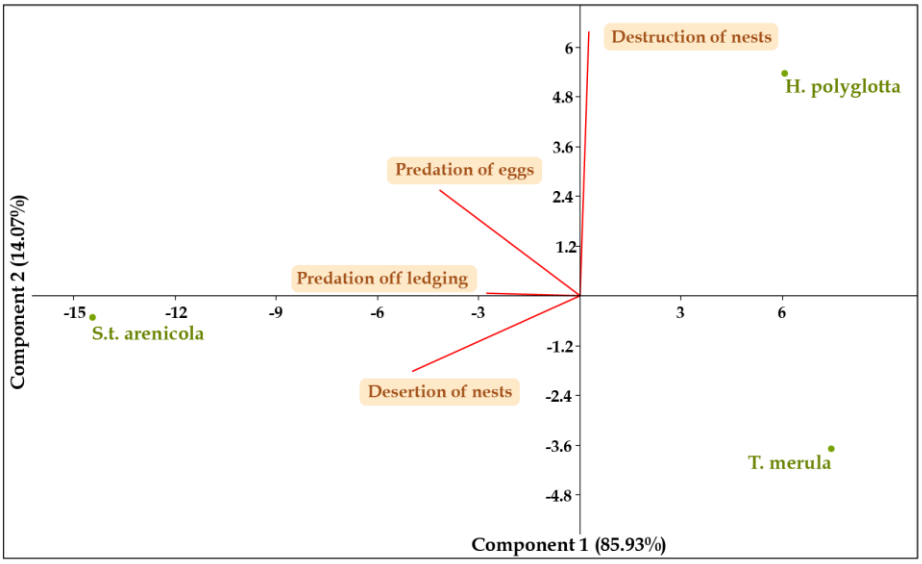

Figure 6 Principal factors affecting the nests of the studied species in the riparian vegetation of the upper Moulouya Mountains analyzed with PCA (2D plot).

3.5. Effect of habitat features on nest success

The predictors of breeding success in the studied birds are presented in Table 4. Habitat variables affected the breeding success of nesting species differently in the High Moulouya River. In breeding *H. polyglotta,* breeding success was affected by the distance separating the nest location from the nearest water sources. The nests built close to the streams of rivers were destroyed by the increasing level of flow. The breeding success of *S. t. arenicola* was negatively affected by the presence of human activities (i.e., farmlands) and the nearest roads to nesting sites. The nests of the doves were destroyed by human activities and disturbed by road traffic. The success rate of *T. merula* nests was slightly affected (negative impact) by the distance separating nests from human-made farms. Farmers disturb nests with their agricultural practices. In contrast, the distance separating coexisting nests of conspecific birds (D.N.C.N.) did not affect the breeding success of the studied species.

4. Discission

This paper describes new data on the nest niches and breeding success of passerine (*H. polyglotta* and *T. merula*) and Columbiform (*S.t. arenicola*) birds in Upper Moulouya. We investigated the longitudinal and vertical distributions of nests as well as the breeding success of the studied birds. The obtained results defined the levels of segregation of nesting sites, nest substrate, and placement of nests among these birds in the riparian vegetation of three tributary rivers of Moulouya. Similarly, our results demonstrated the rates of breeding success and controlling factors in the studied birds.

This study recorded for the first time the breeding activity of *H. polyglotta* in Morocco and the entire southern slope of the Mediterranean basin (Prodon and Lebreton 1981; Faivre and Auger 1993). Similarly, we recorded nests of *T. merula* and *S.t. arenicola*. The most important breeding populations were *H. polyglotta,* with 55.47% of nests, followed by *S.t. arenicola,* with 23.57% of nests, and *T.*

merula, with 20.95% of nests. Currently, (Mansouri et al. 2021c; Wakass et al. 2023) mention the presence of *H. polyglotta* as a breeder in the upper Moulouya and Eastern High Atlas (15 km to Upper Moulouya), while (Mounir et al. 2022) record the breeding pairs of this small passerine in the Central High Atlas (150 km to the Upper Moulouya). However, none of these authors have recorded nests of this species in Morocco or North Africa. Concerning the other birds, significant breeding populations of *S.t. arenicola* (467 nests) and *T. merula* (74 nests) were mentioned in apple orchards of the Midelt located in the upper Moulouya (El Hassani et al. 2021; Mansouri et al. 2021c; Mansouri et al. 2021b; Mansouri et al. 2022b). Similarly, (Squalli et al. 2022b) described the breeding of *Streptopelia turtur* and *Turdus merula* in the riparian vegetation of the Moulouya River. In our case, the abundance of nests of *T. merula* and *S.t. arenicola* was principally governed by the abundance of breeding and feeding resources (water in rivers). In fact, (Mansouri et al. 2019; Mansouri et al. 2021a) documented the foraging habitats of the North African subspecies *Streptopelia turtur arenicola* in the riparian sites of the Ansgmir, Moulouya and other rivers of the upper Moulouya. In contrast, the breeding drivers of *H. polyglotta* have not yet been identified.

Table 4 Predictors of breeding success in the studied species analyzed with multiple regression tests (D.H.A: distance to the nearest human activities; D.N.C.N: distance to the nearest coexisting nest of the same species; D.N.W: distance to the nearest water stream; D.N.R: distance to the nearest road).

Species	Predictors	Estimate	Error	Statistic	P Value
H. polyglotta	D.H.A	0.00305795	0.0019046	1.60556	0.1109
	D.N.C.N	-2.5929E-05	0.00019974	-0.129814	0.8969
	D.N.W	-0.00226875	0.00126131	-1.79873	0.0744
	D.N.R	0.00466265	0.00327233	1.42487	0.1566
S. t. arenicola	D.H.A	-0.0218345	0.00625439	-3.49108	0.0007
	D.N.C.N	-0.00022981	0.00044251	-0.519346	0.6048
	D.N.W	0.00802048	0.00453745	1.76762	0.0805
	D.N.R	0.0210635	0.00572137	3.68154	0.0004
T. merula	D.H.A	0.0121659	0.00612785	1.98534	0.056
	D.N.C.N	3.601E-05	0.00011927	0.301912	0.7647
	D.N.W	-0.0048822	0.0028063	-1.73973	0.0918
	D.N.R	0.00425143	0.00273217	1.55606	0.1298

Currently, cohabitation between avian species has received increasing attention, particularly in North African farmlands such as olive groves (Squalli et al. 2022c; Squalli et al. 2022d) and apple orchards (Mansouri et al. 2022b). In our study, we demonstrated that the nests of cohabiting species were distributed differently among the monitored rivers. The majority of *T. merula* nests (66.67%) were built in the upstream zones of rivers rather than in the downstream (21.79%) and intermediate zones (11.54%). In contrast, the majority of *S. t. arenicola* nests (73.74%) were concentrated in the intermediate and downstream areas. On the other hand, nests of *H. polyglotta* were shared between the upstream and intermediate zones. This longitudinal segregation of nesting sites is suggested to reduce the concurrence of nesting resources among cohabiting species, as reported currently in the farmlands of the Saiss Plain (Squalli et al. 2022c) and in the riparian vegetation and apple orchards of the Moulouya High Plain (Mansouri et al. 2021d; Squalli et al. 2022b). Furthermore, (Squalli et al. 2022c; Squalli et al. 2022d) demonstrated that *S. t. arenicola* selects breeding sites far from cooccurring competitors and predators to avoid competition for nesting trees and for the protection of its broods from predators. In our study, nests of *H. polyglotta* and *S. t. arenicola* were commonly constructed on hawthorn (*Crataegus monogyna*) and wild rose (*Rosa canina*), while the other species, *T. merula*, prally selected trees of *Salix* sp. and *Poplar* sp. for nesting. Similar results have been reported for the riparian vegetation of upper Moulouya streams; nests of *S. t. arenicola* have been found on trees of wild rose (Squalli et al. 2022b). Equally, nests of the studied species were segregated vertically, which represents another level of habitat partitioning. The vertical separation of nests was observed in the breeding colony of six heron species that nest in pitch pine trees (*Pinus rigida*): *Nycticorax nycticorax, Bubulcus ibis, Egretta alba, Egretta intermedia, Egretta garzetta,* and *Ardea cinerea* (Park et al. 2011). The breeding species vertically stratify the nest placements according to their body size, except for *Bubulcus ibis* and *Nycticorax nycticorax*, which nest at sites higher than those predicted based on their body size. In our case, the vertical and longitudinal segregation of nest niches suggested that aggressive interspecific interactions among neighbors influence nest site selection to enhance breeding success. Similar results were demonstrated in *S.t. arenicola* near the Fez urban zone, where it selects elevated placement for its nests far from neighboring predators and competitors to ensure better productivity (Squalli et al. 2021; Squalli et al. 2022d).

In this study, we presented new data on the productivity and factors controlling the breeding success of birds in riparian ecosystems of the upper Moulouya Mountains. Breeding success was superior in *T. merula* and *H. polyglotta,* while productivity was inferior in *S. t. arenicola*. Furthermore, nests of *S. t. arenicola* were impacted by predation, which affected nests during the laying and hatching stages and caused the desertion of clutches. Nests of *H. polyglotta* were principally impacted by destruction. Currently, (Mansouri et al. 2021d) reported a productivity rate of 53% in riparian vegetation and 57% in the apple groves of Moulouya for *S.t. arenicola*, which is similar to our results. The same author mentioned predation (33.16% of clutches) and desertion (21.33% of clutches) as principal factors of failure in vulnerable Columbidae (Mansouri et al. 2021d). (El Hassani et al. 2021) reported a breeding success of 69.03% in *T. merula* on the Moulouya High Plain, which is inferior to our results. For *H. polyglotta,* our results concerning breeding success are the first in Morocco and the entire North Africa. Similarly, the breeding success of *S. t. arenicola* was affected by human activities (i.e., farmlands) and distance to the nearest roads, which is in agreement with results currently reported by (Mansouri et al. 2021d) in riparian vegetation of the upper Moulouya and results mentioned by (Squalli et al. 2022d) in olive groves of the Saiss Plain. Generally, this vulnerable Columbidae species selects nesting sites in ecosystems located in or near farmlands but far from human disturbance, such as roads and human infrastructure, to protect its broods and ensure higher breeding success (Mansouri et al. 2022b; Squalli et al. 2022d). In the same way, breeders of *T. merula* selected nests near human-made farms, which increased their breeding success (Mansouri et al. 2022a). In the breeding of *H. polyglotta,* this study demonstrated for the first time that breeding success was related to the distance between the nest location and the nearest water source. This suggests that the availability of the nearest water sources is necessary to ensure the forage of broods and therefore to ensure successful breeding. In contrast, higher river flow leads to the destruction of *H. polyglotta* nests.

5. Conclusions

In summary, this study highlighted new data on nest-niche ecology and the breeding success of three avian species in Morocco and North Africa. Our results revealed important breeding populations of *S. t. arenicola, H. polyglotta,* and *T. merula* in the riparian vegetation of the upper Moulouya rivers. Furthermore, we demonstrated nesting habitat selection, levels of segregation and cohabitation, and rates of success among the studied birds. The nests of the breeding species were distributed along the river sections, and the nesting trees were partially segregated among the studied species. Similarly, the nests of the three species were segregated to reduce competition for nesting resources. On the other hand, the surveyed birds showed different rates of breeding success, which were affected by human and natural factors such as the availability of foraging resources and the impact of human disturbance. Finally, this study provides new insight into breeding birds in the riparian vegetation of rivers in Morocco and the entire region of North Africa. However, future investigations are required to understand the main reasons behind the drivers of the selection of nesting habitats by avian species, particularly passerines. Furthermore, the characterization of the nesting sites, breeding ecology, and productivity of *H. polyglotta* is suggested to fill the gap in data on North African birds.

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Ethical considerations

Not applicable.

Conflict of interest

The authors declare that they have no competing interests.

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