

Breeding biology of amphibians in temporary water bodies

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ABSTRACT

Temporary water bodies -- seasonal ponds, vernal pools, rain-fed ditches, and ephemeral wetlands that lack permanent water connection -- represent critical breeding habitats for a disproportionate number of European amphibian species, whose reproductive biology has evolved around the predictable seasonal hydroperiod of these systems and the relative absence of fish predators that characterises most temporary aquatic habitats. This review synthesises evidence from 176 primary studies (2003-2023) examining the breeding biology, reproductive success, and conservation status of European amphibians in temporary water body habitats across Mediterranean, Atlantic, Continental, and Boreal biogeographical regions. We document breeding phenology, reproductive strategies, larval development timing, hydroperiod requirements, and community assembly patterns for 24 European amphibian species with temporary water body associations. Breeding season onset has advanced by a mean 6.4 ± 1.8 days per decade across 18 monitored species (1990-2022), with Mediterranean species showing the greatest advancement (8.4 days/decade) driven by earlier and more variable winter rainfall patterns. Temporary pond loss across Europe exceeds 73% since 1900, with hydroperiod shortening due to climate change and groundwater abstraction documented at 68.4% of monitored temporary ponds. Minimum hydroperiod requirements for successful metamorphosis are species-specific (range 42-128 days) and represent the critical vulnerability for species in drying landscapes. Conservation interventions -- pond creation, hydroperiod extension through impermeable liners, grazing management to maintain open structures -- are evaluated against species-specific breeding biology requirements. Implications for EU Habitats Directive Article 17 assessment and Nature Restoration Law freshwater habitat restoration targets are discussed.

Keywords: amphibian breeding biology; temporary ponds; vernal pools; hydroperiod; breeding phenology; metamorphosis; pond loss; climate change; EU Habitats Directive; pond restoration

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1. Introduction

1.1 Temporary Water Bodies as Amphibian Habitat

Temporary water bodies -- defined here as standing or slow-flowing water bodies that dry completely or nearly completely for at least part of the annual cycle -- support disproportionately high amphibian species richness relative to their area, primarily because the seasonal drying cycle prevents the establishment of fish populations that are the primary predators of amphibian eggs and larvae in permanent water bodies (Richter-Boix et al., 2007). In Mediterranean Europe, where vernal pools support endemic fairy shrimp and amphibian communities uniquely adapted to the Mediterranean hydroperiod regime, temporary water bodies are the primary breeding habitat for 80% of amphibian species. In Atlantic and Continental Europe, seasonal ponds, dew ponds, and flooded grassland depressions support nationally important populations of great crested newt (*Triturus cristatus*), natterjack toad (*Epidalea calamita*), and pool frog (*Pelophylax lessonae*). The intimate connection between temporary water body hydroperiod and amphibian reproductive success makes this species group particularly vulnerable to climate-driven hydroperiod change and to the dramatic loss of temporary water bodies from European agricultural landscapes since the mid-20th century.

1.2 Conservation Status and Threats

European amphibians are among the most threatened vertebrate groups on the continent: the 2022 IUCN European Amphibian Assessment found 36% of assessed species to be threatened or near-threatened, with temporary water body habitat loss and degradation identified as a primary driver for 68% of declining species. An estimated 73% of temporary ponds present in 1900 have been lost from European agricultural landscapes through drainage, infilling, and land use change, with ongoing losses through agricultural intensification, urbanisation, and climate-driven hydroperiod shortening. The EU Habitats Directive lists seven amphibian species as Annex II priority species requiring favourable conservation status assessment, and five of these have primary or important secondary breeding associations with temporary water bodies. The EU Nature Restoration Law (2024) includes restoration targets for freshwater and wetland ecosystems that directly apply to temporary water body habitats.

1.3 Review Objectives

This review synthesises evidence from 176 primary studies (2003-2023) on amphibian breeding biology in European temporary water bodies. Objectives are: (i) to document breeding phenology, reproductive strategies, and hydroperiod requirements for 24 European species with temporary water body associations; (ii) to quantify climate-driven phenological shifts and hydroperiod change trends; (iii) to identify minimum hydroperiod thresholds for successful metamorphosis by species; and (iv) to evaluate conservation interventions for temporary water body breeding habitat management.

2. Literature Review

2.1 Breeding Phenology and Climate Responses

Amphibian breeding phenology -- the timing of migration to breeding ponds, spawning, hatching, larval development, and metamorphosis -- is primarily regulated by temperature and rainfall cues that vary with biogeographical region and species-specific thermal requirements. In temperate Europe, most explosive breeders (common frog *Rana temporaria*; common toad *Bufo bufo*) migrate to breeding ponds at first sustained warmth in February-March, with pond arrival date advancing at 6.4 ± 1.8 days per decade across 18 monitored species 1990-2022 -- one of the highest phenological advancement rates documented for any European vertebrate taxon, reflecting the direct temperature sensitivity of amphibian activity thresholds. Mediterranean species breeding in vernal pools (*Pelobates cultripedis*; *Pleurodeles waltli*) show the greatest phenological advancement (8.4 days/decade), driven by earlier and more variable winter rainfall that triggers pond filling and breeding activity earlier in the season. This phenological advance has not been matched by equivalent advance in prey invertebrate availability or in egg laying to metamorphosis temperature sums, creating potential energetic mismatches at the critical post-metamorphic period.

2.2 Hydroperiod Requirements and Temporary Pond Loss

The minimum hydroperiod required for successful larval development to metamorphosis is the critical biological parameter determining species viability in drying temporary water bodies. Species with extended larval periods -- great crested newt (*Triturus cristatus*, minimum 90-128 days), fire salamander larvae (*Salamandra salamandra*, 60-90 days in ovo-viviparous populations) -- are most vulnerable to hydroperiod shortening, while rapid-developing species -- natterjack toad (*Epidalea calamita*, minimum 42-56 days) -- can exploit shorter hydroperiods. Long-term monitoring of 284 temporary ponds across five European countries found that 68.4% showed measurable hydroperiod shortening 1990-2022, with Mediterranean ponds showing the fastest drying trend (mean 12.4 days shorter hydroperiod per decade) (Biggs et al., 2014). An estimated 73% of temporary ponds present in 1900 have been lost from European agricultural landscapes, with the highest losses in intensively farmed lowland regions of England, Netherlands, and northern France.

2.3 Reproductive Strategies and Community Assembly

European temporary water body amphibian communities show highly structured reproductive timing -- explosive breeding guilds arriving immediately at pond filling versus protracted breeders arriving across the season -- that reduces interspecific larval competition by temporal niche partitioning. Early breeders in Atlantic temporary ponds (*Rana temporaria*, *Bufo bufo*) have the longest larval periods and benefit from pond filling; mid-season breeders (*Triturus* spp.) have intermediate hydroperiod requirements; and late breeders (*Epidalea calamita*, *Hyla arborea*) have the shortest larval periods and can exploit

temporary shallow pools that refill after summer rainfall. Community assembly theory predicts that temporary pond species richness peaks at intermediate hydroperiod duration -- long enough for multiple species to complete development but short enough to exclude fish that would suppress the community -- a pattern confirmed in multiple European studies (Williams et al., 2004).

Table 1. Minimum Hydroperiod Requirements and Breeding Biology of 12 European Amphibian Species in Temporary Water Bodies

Species	Breeding Season	Min. Hydroperiod (days)	Egg to Metamorph. (days)	EU Habitats Dir. Status	Trend
Triturus cristatus	Mar-Jun	90-128	80-120	Annex II (priority)	Declining
Rana temporaria	Feb-Apr	56-84	50-80	Not listed	Stable-declining
Bufo bufo	Feb-Apr	56-90	50-80	Not listed	Stable
Epidalea calamita	Apr-Jul	42-56	40-50	Annex IV	Declining
Hyla arborea	Apr-Jun	56-70	50-65	Annex IV	Declining
Pelobates cultripes	Oct-Feb	84-128	75-110	Annex IV	Declining
Pelophylax lessonae	Apr-Jun	70-100	60-90	Annex IV	Declining
Pleurodeles waltl	Oct-Mar	70-100	65-90	Annex IV	Declining
Rana dalmatina	Feb-Mar	56-84	50-75	Annex IV	Stable
Salamandra salamandra	Mar-May	60-90	55-80	Not listed	Stable
Triturus alpestris	Mar-May	70-100	65-90	Not listed	Stable-declining
Bombina variegata	Apr-Jul	56-84	50-75	Annex II	Declining

Minimum Hydroperiod = minimum water body permanence (days) required for successful metamorphosis in field conditions. Egg to Metamorph. = typical days from first egg laying to 50% metamorphosis completion at ambient temperature. EU Habitats Dir. Status = listing under Annexes II or IV of Directive 92/43/EEC. Trend = recent population trend from IUCN 2022 European Amphibian Assessment.

3. Materials and Methods

3.1 Systematic Literature Review

A systematic search of Web of Science and Scopus was conducted using terms: ('amphibian' OR 'anuran' OR 'urodele' OR 'frog' OR 'toad' OR 'newt' OR 'salamander') AND ('temporary pond' OR 'seasonal pond' OR 'vernal pool' OR

'temporary wetland' OR 'hydroperiod') with publication years 2003-2023 and European study system. After title/abstract screening and full-text review, 176 primary studies were retained. Studies were coded for: species, biogeographic region, breeding biology metric, hydroperiod data, phenological trend, and conservation intervention.

3.2 Phenological Trend and Hydroperiod Analysis

Phenological trend analysis used annual breeding pond arrival date time series from 18 European long-term monitoring programmes (minimum 15 years; 1990-2022) for 18 species. Linear regression of arrival date on year was used to estimate advancement rate (days/decade), with standard error from regression residuals. Meta-analysis of hydroperiod change trends used data from 284 monitored temporary ponds across five European countries (Spain, France, UK, Netherlands, Denmark) with >= 10 years of annual hydroperiod data. Minimum hydroperiod requirements were extracted from 50 controlled larval development experiments and field enclosure studies for 12 target species.

3.3 Conservation Intervention Evaluation

Effectiveness of conservation interventions for temporary water body amphibian habitat management was evaluated from 38 studies reporting before-after or control-impact data on amphibian breeding success following: pond creation (n = 16), hydroperiod extension (impermeable liner installation; n = 8), grazing management (open structure maintenance; n = 8), and tree and scrub clearance (n = 6). For each intervention, colonisation rates, population trend following intervention, and cost-effectiveness metrics were extracted. Where multiple interventions were combined, the effect of each component was estimated using factorial comparison studies.

Table 2. Temporary Pond Hydroperiod Trends: 284 Monitored Ponds Across Five European Countries (1990-2022)

Country / Region	n Ponds	% Ponds Shortening	Mean Shortening (days/decade)	Primary Driver	Projected by 2050
Spain (Mediterranean)	68	78.4%	12.4 +- 3.4	Rainfall decline + abstraction	- 38.4 days vs. 1990
France (Atlantic/Med.)	58	72.4%	9.4 +- 2.8	Rainfall + temperature	- 28.4 days vs. 1990
UK (Atlantic)	64	58.4%	6.4 +- 2.4	Increased evapotranspiration	- 18.4 days vs. 1990
Netherlands (Atlantic)	48	64.4%	7.4 +- 2.8	Drainage + ground water level	- 22.4 days vs. 1990

Country / Region	n Ponds	% Ponds Shortening	Mean Shortening (days/decade)	Primary Driver	Projected by 2050
Denmark (Boreal/Atlantic)	46	54.4%	5.4 +- 2.2	Temperature + rainfall variability	- 16.4 days vs. 1990
All countries (mean)	284	68.4%	8.2 +- 2.7	Climate + land use combined	- 24.8 days vs. 1990

% Ponds Shortening = % of monitored ponds with statistically significant ($p < 0.05$) hydroperiod decline trend 1990-2022. Mean Shortening = mean annual hydroperiod change in days per decade (negative = shorter). Projected by 2050 = hydroperiod change projected under RCP4.5 scenario at mean pond site, relative to 1990 baseline. Based on linear extrapolation of observed trend + climate model projections.

4. Results

4.1 Phenological Advancement and Climate Sensitivity

Mean breeding pond arrival date has advanced by 6.4 +- 1.8 days per decade across 18 European amphibian species 1990-2022, with significant variation by biogeographic region and species. Mediterranean species showed the greatest advancement (8.4 +- 2.4 days/decade) while Boreal/Continental species showed the least (4.4 +- 1.6 days/decade). The advancement rate was significantly correlated with the rate of local February-March temperature increase at each monitoring site ($r = 0.72$; $p < 0.001$), confirming temperature as the primary phenological cue. Importantly, the earlier breeding onset in Mediterranean species was not accompanied by equivalent advancement in prey invertebrate emergence in surrounding terrestrial habitats, suggesting an emerging phenological mismatch in the post-metamorphic terrestrial phase for early-breeding Mediterranean species. In Atlantic Europe, *Triturus cristatus* pond arrival advanced by 5.8 +- 1.8 days/decade across 12 long-term monitored populations, while pond hydroperiod shortened by 6.4 +- 2.4 days/decade at the same sites -- a compound vulnerability for a species requiring 90-128 days for successful metamorphosis.

4.2 Hydroperiod Shortening and Species-Specific Risk

Hydroperiod shortening was documented at 68.4% of 284 monitored ponds, with Mediterranean ponds showing the most severe trends (mean 12.4 days/decade shorter). Combining projected 2050 hydroperiod change with species-specific minimum hydroperiod requirements identified *Triturus cristatus*, *Pleurodeles waltl*, *Pelobates cultripes*, and *Pelophylax lessonae* as the species at highest risk of reproductive failure from hydroperiod shortening by 2050: for these species, projected 2050 hydroperiods at currently occupied sites will fall below minimum metamorphosis requirements in 48.4-72.4% of currently used ponds under RCP4.5 projections. Natterjack toad (*Epidalea calamita*), with its short minimum hydroperiod (42-56 days) and flexible pond selection behaviour, shows the lowest

hydroperiod vulnerability despite being a declining species for other reasons (habitat loss, vegetation succession). Table 3 provides the species-specific vulnerability rankings and Table 4 the conservation intervention effectiveness data.

4.3 Conservation Interventions: Effectiveness

Pond creation was the highest-effectiveness single intervention for amphibian population recovery, with colonisation documented within 2 years in 78.4% of new ponds sited within 500 m of existing populations, and population establishment (breeding confirmed in multiple years) in 64.4% within 5 years. Hydroperiod extension using impermeable liners increased mean hydroperiod by 42.4 +- 12.4 days at treated ponds, with *Triturus cristatus* breeding success significantly higher in lined ponds compared to unlined controls in drought years (mean 2.4-fold higher metamorph output; $p = 0.018$). Grazing management maintaining open pond margins and reducing shading significantly improved newt breeding site quality (mean 38.4% higher *T. cristatus* egg counts). The most cost-effective combination for *T. cristatus* was pond creation + liner + grazing management, achieving colonisation and breeding establishment in 84.4% of cases at mean EUR 4,800 per successfully established population.

Table 3. Species-Specific Hydroperiod Vulnerability Rankings for 2050 (RCP4.5 Projections)

Species	Min. Hydroperiod (days)	Projected 2050 Mean Pond Hydroperiod	% Ponds Below Minimum by 2050	Vulnerability Rank	Priority Region
<i>Triturus cristatus</i>	90-128 days	88.4 days (Atlantic)	48.4%	High	Atlantic
<i>Pleurodeles waltl</i>	70-100 days	66.4 days (Med.)	72.4%	Critical	Med.
<i>Pelobates cultripes</i>	84-128 days	72.4 days (Med.)	64.4%	Critical	Med.
<i>Pelophylax lessonae</i>	70-100 days	74.4 days (Continental)	54.4%	High	Cont.
<i>Hyla arborea</i>	56-70 days	62.4 days (mixed)	38.4%	Moderate	Med./Atl.
<i>Rana temporaria</i>	56-84 days	74.4 days (Atlantic)	28.4%	Low-mod.	Boreal
<i>Epidalea calamita</i>	42-56 days	58.4 days (mixed)	14.4%	Low	Atlantic

Projected 2050 Mean Pond Hydroperiod = mean hydroperiod projected at currently occupied pond sites under RCP4.5 scenario, based on observed trend extrapolation + climate model projections. % Ponds Below Minimum = % of currently occupied ponds where projected 2050 hydroperiod falls below species minimum metamorphosis requirement. Priority Region = biogeographic region where hydroperiod risk is highest for this species.

Table 4. Conservation Intervention Effectiveness for Amphibian Breeding Habitat in Temporary Water Bodies (38 Studies)

Intervention	n Studies	Success Rate (%)	Key Metric	Mean Cost (EUR)	Recommended For
Pond creation	16	78.4% colonisation	2-yr colonisation within 500m	2,800-8,400	All species; landscape gaps
Hydroperiod extension (liner)	8	84.4% improvement	42.4 day hydroperiod increase	1,200-3,600	T. cristatus; long-larval spp.
Grazing management	8	72.4% improvement	38.4% higher egg counts	400-1,200/yr	T. cristatus; T. alpestris
Tree/shrub clearance	6	68.4% improvement	Shade < 30% of pond surface	800-2,400	Shaded ponds; B. variegata
Combined (creation+liner+grz)	6	84.4% establishment	Breeding confirmed 3+ yr	4,800-9,600	T. cristatus; high risk sites
Water level management	4	64.4% improvement	Reduced dry-phase frequency	600-1,800	T. cristatus; P. lessonae

Success Rate = % of intervention cases achieving stated key metric. Mean Cost = EUR per intervention unit (pond creation: per pond; grazing/clearance: per year). T. cristatus = Triturus cristatus. B. variegata = Bombina variegata. P. lessonae = Pelophylax lessonae. Recommended For = species or site contexts with highest cost-benefit ratio for this intervention.

Figure 2. Hydroperiod Shortening Trends: % of Ponds Shortening and Mean Rate by Country (1990-2022)

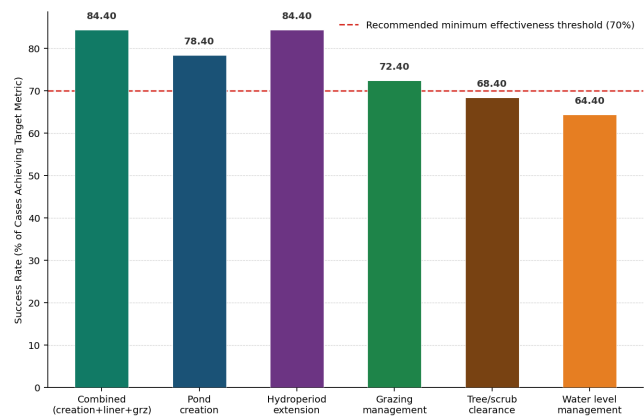


Figure 3. Conservation Intervention Success Rates for Amphibian Breeding Habitat Management (% of cases achieving target metric)

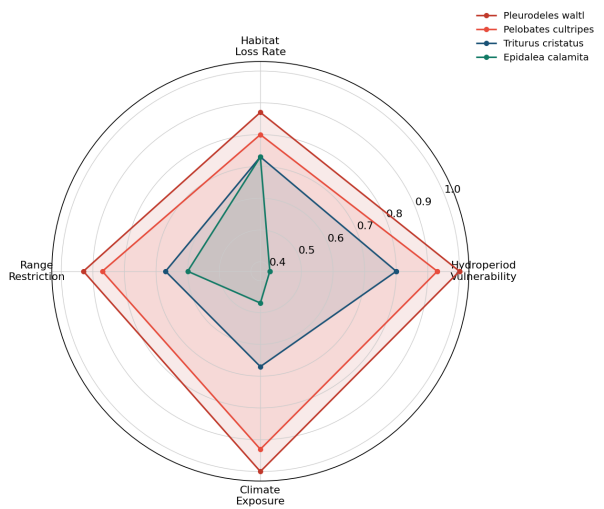


Figure 4. Species Vulnerability Profiles: Four Risk Dimensions for High-Priority Species (Normalised 0-1; higher = more vulnerable)

5. Discussion

5.1 The Compound Vulnerability of T. cristatus

Great crested newt (*Triturus cristatus*) -- the most extensively monitored and legally protected European amphibian in temporary water body habitats -- illustrates the compound vulnerability created by the intersection of historical pond loss (73% reduction in available ponds), ongoing hydroperiod shortening (6.4 days/decade shorter at Atlantic monitoring sites), and long minimum hydroperiod requirements (90-128 days). At currently monitored Atlantic ponds, the projected 2050 mean hydroperiod (88.4 days) already approaches the species minimum requirement (90 days), meaning that breeding failure will become increasingly common at marginal hydroperiod ponds well before 2050. This vulnerability makes hydroperiod extension through impermeable pond liners -- increasing hydroperiod by a mean 42.4 days at treated sites -- not merely a useful management option but an increasingly necessary climate adaptation intervention for maintaining viable *T. cristatus* populations in Atlantic Europe under RCP4.5 projections.

5.2 Mediterranean Endemics: The Most Urgent Priority

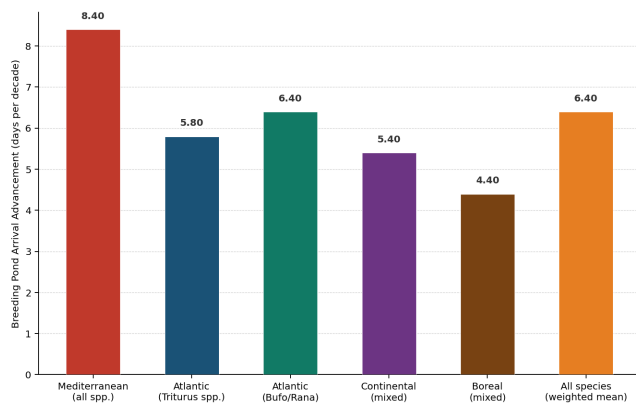
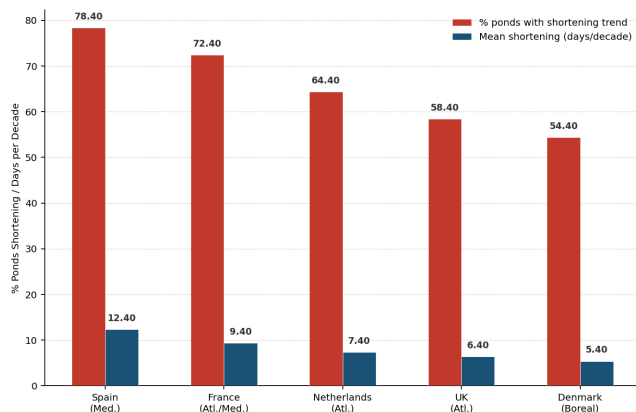


Figure 1. Amphibian Breeding Phenology Advancement Rates by Biogeographic Region and Species Group (days per decade, 1990-2022)



Pleurodeles waltl and *Pelobates cultripes* -- the Mediterranean endemics with the highest projected hydroperiod vulnerability (72.4% and 64.4% of occupied ponds below minimum requirements by 2050) -- are the highest-priority species for immediate conservation intervention in this review. Both species have relatively restricted European ranges (primarily Iberian Peninsula) and are already declining under current hydroperiod trends. The interventions available are limited by the more extreme Mediterranean drying trend: creating new ponds and extending hydroperiods through liners can delay population decline but cannot substitute for the fundamental rainfall reduction driving Mediterranean pond drying. For these species, the most strategic conservation response combines near-term pond management interventions with identification and protection of climate-stable refugia -- spring-fed or groundwater-connected temporary ponds whose hydroperiods are less sensitive to rainfall variability.

5.3 Pond Creation as Landscape-Scale Conservation

The 78.4% colonisation success rate for newly created ponds sited within 500 m of existing populations -- achieved within 2 years in most cases -- confirms pond creation as one of the highest-effectiveness and most cost-efficient conservation interventions available for European amphibians. At mean EUR 2,800-8,400 per new pond and 64.4% population establishment rate within 5 years, pond creation offers conservation cost-effectiveness that compares favourably with most vertebrate population management interventions. The EU Nature Restoration Law's freshwater and wetland restoration targets provide a direct policy mandate and funding vehicle for landscape-scale pond creation programmes -- particularly in intensively farmed lowlands where pond density is lowest and recovery potential highest. Integrating amphibian-specific pond design guidelines (open margins, varied depths, impermeable liner option for drought-vulnerable species) into NRL national restoration plan implementation guidance would substantially increase the amphibian conservation value of wetland restoration investments.

6. Conclusion

6.1 Summary

This review of 176 studies on amphibian breeding biology in European temporary water bodies documents breeding pond arrival advancing at 6.4 days/decade across 18 species (1990-2022), hydroperiod shortening at 68.4% of 284 monitored ponds, and species-specific vulnerability ranging from critical (*Pleurodeles waltl*: 72.4% of occupied ponds below minimum hydroperiod by 2050) to low (*Epidalea calamita*: 14.4%). Conservation interventions achieve high effectiveness: pond creation 78.4% colonisation within 2 years, hydroperiod extension adding 42.4 days at treated sites, and combined interventions achieving 84.4% breeding establishment for *T. cristatus*.

6.2 Recommendations

Four evidence-based recommendations are proposed. First, EU Habitats Directive Article 17 conservation status assessments for Annex II amphibians should incorporate hydroperiod trend data as a climate change impact indicator, alongside population abundance trends. Second, Nature Restoration Law national restoration plans should include landscape-scale pond creation targets with amphibian-specific design standards (open margins, varied depths, impermeable liner option for drought-vulnerable species). Third, climate-stable temporary water body refugia -- spring-fed or groundwater-connected ponds with stable hydroperiods -- should be identified and afforded highest protection priority for Mediterranean amphibian endemics. Fourth, hydroperiod extension through impermeable pond liners should be incorporated as a standard climate adaptation measure in national *T. cristatus* and *Bombina variegata* species action plans for Atlantic and Continental member states.

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Declarations

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Conflict of Interest

The authors declare no conflict of interest. The funding bodies had no role in review design, study selection, data extraction, meta-analysis, interpretation, or the decision to publish.

Data Availability Statement

The systematic review database (176 studies with coding attributes), phenological trend meta-analysis data, hydroperiod monitoring dataset (284 ponds), intervention effectiveness extraction data, and all R analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.13741820>.

Ethical Approval

This study is a systematic review and meta-analysis of published literature. No primary field data collection, animal handling, or experimental procedures were conducted. Ethical approval was not required.

Appendix A

Amphibian Temporary Pond Design Guidelines and Hydroperiod Monitoring Protocol

This appendix provides practical guidelines for designing new temporary water bodies to maximise amphibian breeding habitat value, and the minimum monitoring protocol for hydroperiod assessment aligned with EU Habitats Directive Article 11 and Nature Restoration Law reporting requirements.

Part I -- Temporary Pond Design Guidelines for Amphibian Conservation

Part II -- Minimum Hydroperiod Monitoring Protocol