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Contrasting species- and trait-specific effects of deer wallows on life-history performance in two amphibians

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Abstract

Ecosystem engineers create or modify habitats and can thereby affect the populations of associated species. Although these effects have often been evaluated using abundance-based measures, the survival and growth of individuals within engineered habitats offer a different perspective on the potential significance of these habitats for populations. Yet such fitness-related performance has rarely been compared directly between engineered and non-engineered habitats. Here, we compared the larval survival and growth of two amphibian species (*Rana pirica* and *Hynobius retardatus*) utilizing wallows created by sika deer (*Cervus nippon yesoensis*) with their performance in natural ponds. Our survey revealed that *R. pirica* survived better in wallows than in ponds (mean larval survival: 28.6% vs. 9.9%), whereas *H. retardatus* survived better in ponds than in wallows (30.4% vs. 8.5%). Additionally, in wallows, *R. pirica* reached metamorphosis at a smaller body size (13.0 vs. 14.9 mm) and took longer to metamorphose (86.8 vs. 76.3 days). These results show that engineered habitats do not have uniformly positive or negative effects on associated species: their effects can differ between species and between life-history components. Our study demonstrates that evaluating multiple aspects of individual performance can reveal contrasting effects of engineered habitats that would be overlooked when relying on a single response.

Introduction

Ecosystem engineers are organisms that modify resource availability for other species by physically altering the environment (Jones et al. 1994, 1997). Through such engineering activities, they can profoundly impact local biodiversity by increasing habitat heterogeneity, modifying thermal or moisture regimes, and creating novel habitats for associated species (Coggan et al. 2018). One prominent example is the beaver (*Castor* spp.), which constructs dams that provide valuable habitat for a wide range of aquatic and riparian organisms, including insects, fish, amphibians, and birds (Brazier et al. 2021). Similarly, the massive communal nests of sociable weavers (*Philetairus socius*) create localized biodiversity hotspots by providing refuges for various animals in arid environments (Lowney and Thomson 2021).

The effects of ecosystem engineers on associated populations have often been evaluated by comparing abundance between engineered and non-engineered habitats (Coggan et al. 2018; Mallen-Cooper et al. 2019). However, abundance indicates how many individuals use a habitat, not how that habitat contributes to the population as a whole (Van Horne 1983; Johnson 2007). When a habitat created by an ecosystem engineer is viewed as one of the habitat patches constituting the population of an associated species, evaluating its potential contribution to the population requires information not only on the number of individuals using the patch, but also on how well they survive and grow within it. For example, an engineered habitat supporting many individuals would not necessarily contribute positively to the population if survival is low or growth is poor. Conversely, an engineered habitat used by relatively few individuals could still make a positive contribution if it provides favorable conditions for survival and growth. Survival and growth therefore provide fundamental information for evaluating the potential

contribution of engineered habitats to associated populations, although their actual contribution ultimately also depends on processes such as density dependence and movement among habitats (Pulliam 1988; Rodenhouse et al. 1997; Figueira and Crowder 2006; Dallas et al. 2020). Nevertheless, few studies have directly compared survival and growth between engineered and non-engineered habitats (but see Nummi and Hahtola 2008; Fuller and Peckarsky 2011; Ransom 2012).

Large mammals are well recognized as important ecosystem engineers because they can substantially modify environments through strong per capita engineering effects and their tendency to act collectively (Naiman 1988; Jones et al. 1997; Moore 2006). Ungulates such as bison, wild boar, and zebra alter vegetation and soil structure through collective trampling and wallowing behavior, often creating new waterbodies that are subsequently utilized by various organisms for foraging and reproduction (e.g., Beck et al. 2010; Baruzzi and Krofel 2017; Nickell et al. 2018; Wagner et al. 2021). Waterbodies formed through soil disturbance by ungulates often differ from naturally occurring ponds in hydroperiod (Gerlanc and Kaufman 2003) and water chemistry (McDowell 2009). Such differences suggest that the life-history performance of aquatic organisms may also differ between these habitat types. Despite accumulating evidence, we are unaware of any study that has directly tested whether the life-history performance of resident animals differs between ungulate-created waterbodies and naturally occurring ponds.

Amphibians provide an ideal system for comparing life-history performance between engineered and non-engineered habitats. Several lentic-breeding species oviposit in temporary waterbodies, including wallows created by ungulates (Gascon and Zimmerman 1998; Gerlanc and Kaufman 2003; Beck et al. 2010; Ringler et al. 2015; Baruzzi and Krofel 2017). Their larvae typically remain within a single waterbody until metamorphosis, which allows survival and growth to be tracked under natural conditions. Moreover, larval traits are highly sensitive to local environmental factors (e.g., Newman 1989, 1992; Spieler and Linsenmair 1997; Murphy 2003). These early-life conditions can have lasting effects on post-metamorphic performance, including adult survival and fecundity, thereby influencing population dynamics (Semlitsch et al. 1988; Berven 1990; Newman 1992; Altwegg and Reyer 2003; Wells 2007).

In this study, we compared the survival and growth of two amphibian species during their early life stages between wallows created by the Ezo sika deer (*Cervus nippon yesoensis*) and natural, non-engineered ponds. We also explored potential factors underlying differences between these habitat types. Specifically, we addressed the following three questions: (1) How do environmental conditions differ between deer wallows and natural ponds used by amphibians? (2) Do larval survival and growth differ between habitat types? and (3) Which factors account for any observed differences in larval survival and growth between habitat types?

Materials and methods

Study site

Our study was conducted between October 2021 and July 2022 in the floodplain of a watershed along the Horonai River (42°40'N, 141°35'E), Hokkaido, Japan. Surveys targeted the natural floodplain within the uppermost 6.6 km reach, which contains 93.7% (74 of 79) of all waterbodies (Fig. 1a). Downstream of this reach, the river has been modified, resulting in minimal floodplain area and fewer waterbodies.

Sika deer as ecosystem engineers

The Ezo sika deer (*Cervus nippon yesoensis*) is a subspecies of the sika deer (*C. nippon*) endemic to Hokkaido and is widely recognized as a prominent ecosystem engineer (Wen et al. 2024). The adult males create wallows as part of their breeding behavior through vigorous soil excavation (Miura 1985). During this process, they paw and thrash the ground violently with their antlers or forefeet, followed by lying down and rubbing their bodies against the ground (Online Resource 2). In low-lying wet areas such as floodplains, these wallows are frequently reused by multiple individuals, resulting in deep depressions that consistently accumulate water. Although wallowing is limited to the autumn breeding season from September to December, the resulting excavations persist for extended periods (Miura 1985; Comte et al. 2022). By the following spring, many of these depressions remain water-filled and serve as breeding sites for amphibians.

The ecological impact of sika deer is amplified by their rapid population expansion across Japan (Iijima et al. 2023), similar to trends in the United States and the United Kingdom (Wildlife Informer 2021; The British Deer Society 2023). Near the study area in Hokkaido, density was previously estimated at 3.8 ± 3.4 (mean ± SD) individuals km^{-2} in 2001 (Agetsuma et al. 2002). Given continued regional population growth, local density during the present study likely surpassed this historical baseline (Agetsuma 2018; Hokkaido Government 2025).

Two amphibians utilizing engineered habitat

The Ezo brown frog (*Rana pirica*) and the Ezo salamander (*Hynobius retardatus*) are common amphibians in Hokkaido that utilize various lentic waterbodies, including wallows, for spring spawning. Each female *R. pirica* deposits an egg mass containing hundreds of eggs in shallow water less than 10 cm deep, often forming aggregative clusters (Fig. S1, Online Resource 1). Their larvae hatch within two weeks and metamorphose approximately two months later. *Hynobius retardatus* spawn a pair of egg sacs containing dozens to a hundred eggs (Fig. S2, Online Resource 1). These egg sacs are attached to submerged objects, such as fallen branches, at depths of 10–100 cm. The eggs hatch within several weeks, and larvae develop in the water for several months before transitioning to land. Although some larvae delay metamorphosis for multiple years (Kanki and Wakahara 2001), this was rarely observed at our study site. *Hynobius retardatus* larvae can prey on *R. pirica* larvae, although the strength of this interaction may vary depending on local ecological conditions (Takatsu and Kishida 2015).

Identification of waterbodies and spawning surveys

In October 2021, wallows were initially identified by locating soil depressions with fresh traces of sika deer digging (Supplementary Methods S1, Online Resource 1; Online Resource 2). As other wallowing ungulates are absent from the study area, these depressions were identified as engineered products of sika deer. In March 2022, just before amphibian spawning, we surveyed the entire study area to confirm these sites as water-filled wallows and to locate additional natural ponds (Fig. 1b, c). During the spawning period (late March to May 2022), all waterbodies were surveyed every two to three days to record egg clutches of *R. pirica* and *H. retardatus*. Due to logistical constraints, subsequent surveys were restricted to waterbodies where oviposition was confirmed. Thus, the environmental comparisons between ponds and wallows presented below characterize waterbodies used as spawning sites, rather than ponds and wallows across the entire study area (see Discussion).

Environmental properties of waterbodies

To characterize the environmental properties of ponds and wallows, we monitored environmental variables at all waterbodies where oviposition was confirmed. On 11-April-2022, near the onset of spawning, we quantified hydrogeomorphic variables, including water surface area, central water depth, spring inflow (identified from localized temperature differences and visible groundwater seepage from waterbody margins), and stream connectivity (presence or absence of surface-water connection to the stream). Additionally, we monitored other environmental variables, including desiccation, water temperature, pH, electrical conductivity (EC), and dissolved oxygen (DO). Desiccation was recorded as a binary variable, defined by the occurrence of drying at least once between April and May 2022. Water temperature and chemistry were measured four times (01–02-April-2022, 11-April-2022, 26-April-2022, and 22-May-2022). Dragonfly naiad density was also quantified as an index of potential predation pressure on amphibian larvae. Detailed measurement protocols are provided in Supplementary Methods S2.

Survival of two amphibians

We evaluated two survival indicators: hatching probability and larval survival probability. To determine hatching probability, we examined embryos at the pre-hatching stage (stage 19–20 for *R. pirica* [Gosner 1960] and stage 33–39 for *H. retardatus* [Iwasawa and Yamashita 1991]). Hatching probability was defined as the percentage of surviving embryos relative to the total embryos per clutch. Living and dead embryos were identified based on their shape and color following Okamiya and Kusano (2018). For *R. pirica*, we counted embryos from digital images using ImageJ (version 1.53; https://imagej.nih.gov/ij/index.html). We excluded egg masses that had already hatched or were more than 70% obscured by mud. For *H. retardatus*, embryos were counted by gently lifting egg sacs underwater. We examined all egg sacs in waterbodies containing 50 or fewer egg sacs (16 out of 18 sites); otherwise, we randomly sampled 25% of the total sacs.

We estimated larval survival probability from hatching to the mid-larval stage, at which larvae are capable of fully independent feeding and swimming (≥ stage 25 for *R. pirica* and ≥ stage 44 for *H.*

retardatus). This probability was defined as the percentage of larvae surviving to the mid-larval stage relative to the total hatchlings within each waterbody. Total hatchlings were estimated by multiplying the mean number of hatched individuals per clutch by the total number of clutches. To quantify the number of surviving larvae, we conducted capture surveys during the mid-larval stage (3–5-June for *R. pirica*; 7–8-July for *H. retardatus*). We used either the quadrat or the total-capture method, depending on waterbody size. For the quadrat method, the number of quadrats (0.6 × 0.6 × 0.6 m) was adjusted according to the surface area of each waterbody to ensure representative sampling. The total number of larvae was estimated based on mean larval density across quadrats and the water surface area measured at the time of the capture survey. The total-capture method was applied to waterbodies too small for a quadrat. Methodological differences were confirmed to have minimal impact on survival estimates (see Supplementary Methods S3, Fig. S3, Online Resource 1).

Growth of R. pirica

We quantified three metrics for *R. pirica*: larval size, metamorphic size, and days until metamorphosis. For *H. retardatus*, these metrics were not examined due to extremely high larval mortality in wallows, making comparative analysis unfeasible. During the larval catching survey for *R. pirica*, we photographed a subset of caught individuals (mean ± SD: 20.0 ± 8.03 individuals) and measured larval size as body length (snout to the posterior point of the body, excluding the cloacal tailpiece) using ImageJ. Metamorphosis surveys were conducted weekly between 19-June and 8-July. We photographed pre-metamorphic individuals (stages 38–41) to measure metamorphic size as body length via ImageJ (12.1 ± 10.7 individuals per waterbody). Individuals at stage 42 or later were excluded because body length decreases during final metamorphic remodeling. Days until metamorphosis were calculated as the duration from the median oviposition date to the date when the first metamorphosed individual was recorded.

Statistical analysis

To characterize the waterbodies used as oviposition sites, we compared environmental variables between habitat types (pond vs. wallow) (Question 1). To account for intercorrelations, we performed Factor Analysis of Mixed Data (FAMD) on a set of continuous and categorical variables, incorporating water surface area, depth, the presence of spring inflow, stream connectivity, water temperature, chemistry (pH, EC, and DO), desiccation occurrence, and dragonfly naiad density. For water temperature and chemistry, which were measured on four occasions, we used site-specific estimates adjusted for survey occasion and time of day to characterize environmental differences among waterbodies. The first three FAMD dimensions were retained as major environmental gradients. Differences in FAMD scores between habitat types were tested using linear models (LMs).

We next evaluated whether life-history performance differed between habitat types (Question 2). We used generalized linear mixed models (GLMMs) for hatching probability and linear mixed models (LMMs) for larval and metamorphic size, including waterbody identity as a random effect to account for the non-independence of multiple clutches or individuals within a single waterbody. Generalized linear

models (GLMs) were used for larval survival probability and days until metamorphosis. For hatching and larval survival probabilities, a beta-binomial distribution was used for errors; larval size, metamorphic size and days until metamorphosis were modeled using a normal distribution for errors.

To address Question 3—which factors account for any observed differences in larval survival and growth between habitat types?— we evaluated two relationships for each candidate factor. First, we examined whether the factor differed between ponds and wallows; for environmental factors, this was evaluated in the analyses for Question 1, whereas hatchling density was compared separately below. Second, we examined whether the factor was associated with survival or growth among waterbodies, as described below. Factors showing corresponding patterns in both analyses were considered potential factors underlying habitat-type differences in life-history performance. Although these relationships could in principle be evaluated simultaneously using a multivariate framework such as structural equation modeling (SEM), the limited number of waterbodies precluded reliable estimation of a model with multiple hypothesized pathways. We therefore evaluated the two relationships separately.

As candidate factors, we considered the environmental gradients represented by the FAMD axes and, for post-hatching responses, hatchling density. Hatchling density may influence post-hatching survival and growth through density-dependent interactions, such as conspecific competition and potential heterospecific predator–prey interactions. Because hatchling densities arose from spawning and hatching outcomes, they were not included in the FAMD. We therefore compared hatchling densities between ponds and wallows separately using LMs. Hatchling density was calculated by dividing the estimated total number of hatchlings described above (see Survival of two amphibians) by water volume. Water volume (*V*) was approximated as $V = 0.5AZ$, assuming a paraboloid basin shape, where A is water surface area and *Z* is water depth measured at the center of the waterbody. Because water surface area and depth were not quantified during each hatching survey, we used measurements taken on 11 April, which provided the temporally closest standardized volume measurements available for both species.

We then examined which candidate factors explained differences in survival or growth among waterbodies. We used the same response variables, error distributions, and random-effect structures as in the habitat-type models for Question 2, with the FAMD axes used as explanatory variables. For hatching probability, we used FAMD axes derived from environmental data collected during the pre-hatching period (1–2 and 11 April for *R. pirica*; 11 and 26 April for *H. retardatus*), as hatching success is primarily influenced by conditions prior to hatching (Supplementary Methods S4, Online Resource 1). For post-hatching responses (larval survival probability in both species, and larval size, metamorphic size, and days until metamorphosis in *R. pirica*), we used FAMD axes derived from environmental data collected over the full study period. We additionally included hatchling densities of both species as explanatory variables. Density variables were log-transformed and standardized prior to analysis. All model formulations are provided in Table S1 (Online Resource 3). All data were analyzed using R (Version 4.5.2; R Core Team 2025).

Results

Waterbody identification and spawning records

Across the study area, 74 waterbodies were identified, consisting of 40 ponds and 34 wallows (Fig. 1a; Table S2, Online Resource 3). *Rana pirica* spawning was recorded in 24 ponds (total 260 clutches; mean ± SD: 10.83 ± 12.32) and 7 wallows (total 11 clutches; mean ± SD: 1.57 ± 1.51) (Fig. 2a). *Hynobius retardatus* spawning occurred in 11 ponds (total 303 clutches; mean ± SD: 27.55 ± 38.61) and 7 wallows (total 13 clutches; mean ± SD: 1.86 ± 1.21) (Fig. 2b). The two species co-occurred at 10 ponds and 3 wallows.

Environmental characteristics of oviposition sites across habitat types (Question 1)

Wallows primarily differed from ponds along the second FAMD axis (Dim2), with no significant differences found along the first (Dim1) or third (Dim3) axes. The first three FAMD axes explained 29.4%, 23.1%, and 12.3% of the environmental variation, respectively. Dim2 represented a hydroperiod stability gradient; wallows had significantly higher Dim2 scores (Fig. 3; LM with habitat coded as wallow = 1 and pond = 0: estimate = 1.37, 95% CI = 0.25 to 2.48, $P = 0.018$), indicating greater stream connection, spring presence, lower desiccation risk, shallower depth, and elevated EC. Dim1 was positively associated with pH, DO, water surface area, and stream connection. Dim3 was positively associated with dragonfly naiad density and water temperature.

Survival and growth across habitat types (Question 2)

Regarding the survival of the two amphibians, hatching probability did not differ significantly between ponds and wallows for either species (Fig. 4a, c; Table S3, Online Resource 3; GLMM; *R. pirica*: $P = 0.652$; *H. retardatus*: $P = 0.901$). In contrast, larval survival probability differed significantly between habitat types for both species. For *R. pirica*, survival was higher in wallows (mean ± SD: 28.6 ± 29.1%, $N = 7$) than in ponds (9.9 ± 15.3%, $N = 21$) (Fig. 4b; GLM: estimate = 1.43, 95% CI = 0.46 to 2.41, $P < 0.01$). Conversely, *H. retardatus* showed lower survival in wallows (8.5 ± 18.8%, $N = 6$) than in ponds (30.4 ± 25.3%, $N = 9$) (Fig. 4d; GLM: estimate = − 1.78, 95% CI = − 3.43 to − 0.13, $P = 0.035$).

Regarding *R. pirica* growth, larval size was marginally smaller in wallows (10.6 ± 2.21 mm, $N = 7$) than in ponds (12.3 ± 2.26 mm, $N = 16$) (Fig. 5a; LMM: estimate = − 1.98, 95% CI = − 3.85 to − 0.11, $P = 0.051$). Metamorphic size was significantly smaller in wallows (13.0 ± 1.23 mm; $N = 6$) than in ponds (14.93 ± 2.23 mm; $N = 17$) (Fig. 5b; LMM: estimate = − 1.84, 95% CI = − 3.27 to − 0.40, $P = 0.020$). Days until metamorphosis were significantly longer in wallows (86.8 ± 3.60 days; $N = 6$) than in ponds (76.3 ± 10.5 days; $N = 17$) (Fig. 5c; LM: estimate = 10.54, 95% CI = 1.29 to 19.79, $P = 0.028$).

Factors explaining variation in survival and growth among waterbodies

For *R. pirica*, hatching probability was significantly decreased with higher pre-hatching Dim3 (Table 1; estimate = − 0.41; 95% CI = -0.77 to -0.06; *P* = 0.023; see Supplementary Methods S4, Online Resource 1 for axis interpretation). Larval survival probability significantly increased with higher Dim2 (stream connectivity, spring presence, low desiccation risk, shallow depth, and elevated EC) (estimate = 0.22; 95% CI = 0.005 to 0.44; *P* = 0.045), higher Dim1 (higher pH and DO, and larger water surface area) (estimate = 1.80; 95% CI = 0.87 to 2.73; *P* < 0.001) and higher predatory *H. retardatus* density (estimate = 3.10; 95% CI = 1.37 to 4.84; *P* < 0.001). For *H. retardatus*, hatching probability was not significantly associated with any pre-hatching environmental gradients (Dim1–Dim3), and larval survival probability was not significantly associated with any environmental gradients or hatchling densities of either species (Table 1).

Table 1
Results of regression models examining candidate factors associated with survival in two amphibians. Asterisks indicate significant differences: * for P < 0.05, ** for P < 0.01, and *** for P < 0.001.

R. pirica	**Explanatory variables**	**Estimate**	**Z value**	**P value**
Hatching probability	Dim1	0.012	0.109	0.913
	Dim2	0.141	1.257	0.209
	Dim3	-0.413	-2.269	0.023 *
Larval survival probability	Dim1	1.800	3.814	< 0.001 ***
	Dim2	0.222	2.001	0.045 *
	Dim3	-0.372	-1.624	0.104
	Conspecific density	0.967	1.679	0.093
	H. retardatus density	3.104	3.509	< 0.001 ***
H. retardatus				
Hatching probability	Dim1	0.155	0.556	0.578
	Dim2	0.365	1.188	0.235
	Dim3	-0.195	-0.502	0.616
Larval survival probability	Dim1	0.221	0.263	0.793
	Dim2	-0.379	-1.432	0.152
	Dim3	-0.715	-1.241	0.215
	Conspecific density	1.018	0.487	0.626
	R. pirica density	1.620	1.382	0.167

Table 2
Results of regression models examining candidate factors associated with growth in *R. pirica*.

Larval size	Explanatory variables	Estimate	t value	P value
	Dim1	**1.054**	**1.334**	**0.242**
	Dim2	-0.691	-2.791	0.040 *
	Dim3	0.014	0.026	0.981
	Conspecific density	-0.987	-0.810	0.456
	H. retardatus density	3.905	2.012	0.101
Metamorphic size	Dim1	0.573	1.059	0.332
	Dim2	-0.825	-4.911	0.003 **
	Dim3	0.216	0.593	0.578
	Conspecific density	-0.890	-1.080	0.326
	H. retardatus density	2.983	2.247	0.067
Days until metamorphosis	Dim1	-4.500	-1.347	0.236
	Dim2	2.637	2.528	0.053
	Dim3	-0.779	-0.338	0.749
	Conspecific density	-3.373	-0.653	0.543
	H. retardatus density	-3.701	-0.453	0.669

Regarding *R. pirica* growth, larval size was significantly smaller at sites with higher Dim2 (estimate = − 0.69; 95% CI = − 1.04 to − 0.34; $P = 0.040$). Similarly, metamorphic size was significantly smaller at higher Dim2 (estimate = − 0.83; 95% CI = − 1.08 to − 0.58; $P = 0.003$), but marginally larger at higher *H. retardatus* density (estimate = 2.98; 95% CI = 1.02 to 5.03; $P = 0.067$). Days until metamorphosis marginally increased with higher Dim2 (estimate = 2.64; 95% CI = − 0.04 to 5.32; $P = 0.053$).

Factors explaining habitat-type differences in survival and growth (Question 3)

To identify factors that underlie habitat-type differences in survival and growth, we integrated the results presented above. For *R. pirica*, wallows had higher Dim2 scores than ponds, and higher Dim2 scores were associated with greater larval survival, smaller larval and metamorphic sizes, and a longer time to metamorphosis. These corresponding patterns suggest that the environmental conditions represented by Dim2—greater stream connectivity and spring presence, lower desiccation risk, shallower water, and higher EC—may underlie both the higher survival and the smaller body size and delayed metamorphosis of *R. pirica* in wallows. Although *H. retardatus* hatchling density was positively associated with larval

survival of *R. pirica*, hatchling densities did not differ significantly between ponds and wallows (LM with habitat coded as wallow = 1 and pond = 0: *R. pirica*: estimate = 0.55, 95% CI = -0.36 to 1.47, $P = 0.220$; *H. retardatus*: estimate = 0.20, 95% CI = -0.88 to 1.28, $P = 0.704$). Thus, hatchling density was not supported as a factor explaining the higher *R. pirica* survival in wallows. For *H. retardatus*, neither the measured environmental variables nor hatchling densities were significantly associated with larval survival, and no factor accounting for its lower larval survival in wallows was identified.

Discussion

This study provides a quantitative comparison of the life-history performance of associated species between ungulate-engineered and non-engineered habitats. These results show that engineered habitats do not have uniformly positive or negative effects on associated species. Larval survival of *R. pirica* was nearly three times higher in wallows than in ponds, suggesting that wallows can serve as favorable conditions for larval survival. In contrast, *H. retardatus* showed markedly lower survival, with complete mortality in most wallows precluding further assessment of growth. Even for *R. pirica*, however, smaller larval size and delayed metamorphosis indicate that wallows, while promoting survival, may be suboptimal habitats for growth. Thus, the suitability of the same engineered habitat can differ both between species and between survival and growth within a species.

For *R. pirica*, the higher larval survival in wallows was associated with higher scores along the environmental gradient represented by Dim2. Although Dim2 incorporated several environmental variables, reduced desiccation risk was likely particularly important. Indeed, none of the wallows in which *R. pirica* spawned dried out (0/7), whereas 10 of 24 ponds experienced complete desiccation, likely causing substantial larval mortality. Greater connectivity to rivers and the presence of springs associated with higher Dim2 scores may have contributed to this water-level stability. Repeated trampling may further stabilize water levels by reducing drainage through soil compaction (Beck et al. 2010). Higher Dim2 scores were also associated with shallower water and elevated conductivity, although their direct contributions to larval survival remain unclear. Shallow water can provide favorable conditions for larval survival in lentic-breeding anurans (Wells 2007), whereas high conductivity may reflect conditions associated with greater primary productivity and food-resource availability. In addition, dragonfly naiads (Corduliidae, Libellulidae, and Aeshnidae), which are major predators of *R. pirica* larvae (Kishida et al. 2009), were largely absent from wallows (Table S2, Online Resource 3). Although dragonfly naiad density was not significantly associated with survival, their scarcity suggests that wallows may also reduce exposure to aquatic insect predators. Because these habitats were newly created or disturbed during the previous autumn, such aquatic insects may not yet have colonized them. Together, these patterns suggest that reduced desiccation risk, and potentially reduced predation pressure, contributed to the higher survival of *R. pirica* in wallows. Both desiccation and predation are major sources of mortality during the early life history of amphibians (Gascon 1992; Spieler and Linsenmair 1997; Wilbur 1997; Altwegg 2002; Murphy 2003; Wells 2007).

This hydrological advantage, however, does not appear to be a general feature of deer wallows. In contrast to wallows in which *R. pirica* spawned, many wallows without observed oviposition dried out during the study period (personal observation). This pattern suggests that breeding by *R. pirica* was concentrated in a subset of wallows with relatively stable hydrological conditions. Thus, deer wallows may function as suitable breeding habitats for larval survival of *R. pirica* only when they occur under particular hydrological conditions.

In contrast to *R. pirica*, all *H. retardatus* larvae died in most wallows, and none of the measured environmental variables or hatchling densities explained their lower survival in this habitat type. Oviposition in wallows therefore did not indicate that these habitats provided favorable conditions for subsequent larval survival during the study period.

The results for *R. pirica* further suggest that environmental conditions associated with higher survival in wallows may not coincide with those favoring growth. Dim2 scores, which were higher in wallows, were positively associated with larval survival but negatively associated with larval and metamorphic size, while days until metamorphosis tended to increase with Dim2. Thus, Dim2 was associated with opposite patterns in survival and growth, although the specific environmental factors responsible remain unclear because Dim2 integrates multiple variables. One plausible mechanism underlying reduced growth in wallows is limited food availability. Anuran larvae primarily feed on periphyton and associated microbial communities (Montaña et al. 2019). The hydrological connectivity in wallows may restrict periphyton accumulation through physical flushing. In addition, shallow and newly formed waterbodies such as wallows may lack the leaf litter and organic substrates necessary for periphyton growth. Because food resources were not measured directly, however, this hypothesis remains to be tested. An alternative explanation for the smaller mean body size in wallows is size-selective mortality, whereby smaller individuals are preferentially removed in ponds (Takatsu and Kishida 2015, 2020). The absence of larger individuals in wallows (Fig. 5) is consistent with reduced growth, although it does not fully exclude a contribution from size-selective mortality.

The contrasting survival and growth responses also suggest that benefits of engineered habitats during one life-history stage may not persist into later stages. In amphibians, smaller metamorphs are generally more vulnerable during post-metamorphic stages, potentially resulting in lower survival to reproduction (Altwegg and Reyer 2003) and delayed maturation (Berven 1990). Therefore, although survival probabilities during early life history are higher in wallows, this may not necessarily translate into higher overall fitness. Reduced body size may also alter ecological interactions, as body size strongly influences both the identity of interacting species and interaction strength (Kalinkat et al. 2013; Tsai et al. 2016; Takatsu and Kishida 2015, 2020). For instance, smaller *R. pirica* metamorphs may serve as a food resource for small-sized predators that are unable to consume larger individuals. Size differences between engineered and non-engineered habitats may therefore carry over beyond the aquatic stage, with consequences for both lifetime fitness and interactions within the surrounding community.

The observed differences in environmental conditions and amphibian survival and growth between ponds and wallows may reflect both environmental modification by deer and the characteristics of the sites where wallows form. A limitation of this study is that spatial autocorrelation could not be fully controlled due to our reliance on naturally occurring wallows. Wallows utilized by amphibians tended to be concentrated in the upper reaches of the watershed. Even within a relatively small study area, local conditions such as spring inflow and stream connectivity may be spatially structured. Future comparisons matched for site conditions and manipulative experiments are therefore needed to distinguish the role of wallowing-site selection from that of environmental modification through digging and trampling, and to examine how each relates to survival and growth.

Overall, our study shows that the effects of engineered habitats can differ among associated species and among life-history components within a species. These differences cannot be captured by habitat occupancy or abundance alone. By examining survival and growth, our study highlights the importance of evaluating individual performance as a fundamental component for understanding the potential population-level roles of engineered habitats. However, individual performance within a habitat alone does not determine its contribution to a population. Metapopulation theory emphasizes that population persistence depends not only on the quality of individual habitat patches, but also on their number, spatial distribution, and connectivity (Pulliam 1988; Figueira and Crowder 2006; Dallas et al. 2020). In our study, deer wallows occurred and were used for breeding even in the upper reaches where ponds were scarce, suggesting that ecosystem engineering may alter not only the quality and quantity of breeding habitats but also their spatial configuration across the landscape. Thus, understanding the population-level consequences of engineered habitats requires considering both individual performance within these habitats and how the habitats modify the spatial network of breeding sites. Future studies should examine how these two components jointly influence population dynamics through dispersal among habitats, subsequent life-history stages, and density-dependent processes.

Declarations

Conflict of interest

The authors declare that they have no conflicts of interest to disclose.

Ethics approval

Our work conforms to the guidelines for the proper conduct of animal experiments in Japan and was approved by the committee for animal experiments in FSC of Hokkaido University (ID2-5).

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Authors’ contributions

NM, HO, and OK conceived the ideas and methodology; NM, HO, and OK carried out the survey; NM analyzed data support from AT; NM, HO, and OK wrote the first draft of manuscript. All authors contributed critically to drafts and gave final approval for publication.

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Authors’ contributions

NM, HO, and OK conceived the ideas and methodology; NM, HO, and OK carried out the survey; NM analyzed data support from AT; NM, HO, and OK wrote the first draft of manuscript. All authors contributed critically to drafts and gave final approval for publication.

Availability of data and material

All data analyzed in this study are available at the following site: https://www.dropbox.com/scl/fo/r46raicvf7ixqqulmiq7n/h?rlkey=s4ux25og2xhuio0v3v678z5wj&dl=0.

Code availability

R scripts used for the analyses are available at the following site: https://www.dropbox.com/scl/fo/r46raicvf7ixqqulmiq7n/h?rlkey=s4ux25og2xhuio0v3v678z5wj&dl=0.

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Figures

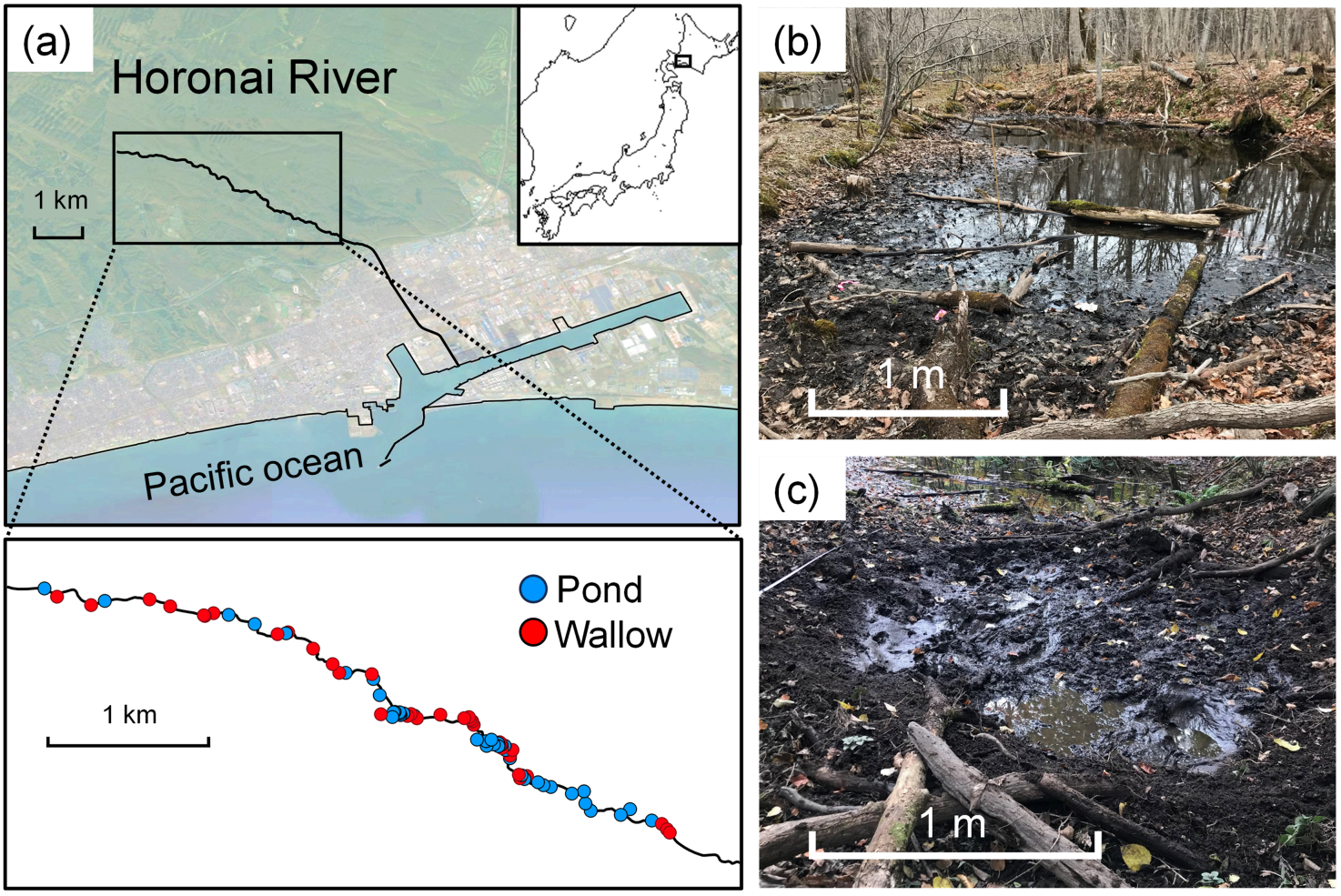


Figure 1

(a) Map of the Horonai River and location of waterbodies within the survey area (i.e., the upstream 6.6 km stretch, where 93.7% (74 of 79) waterbodies were present). The blue circles and the red circles represent ponds (*N* = 40) and wallows (*N*= 34), respectively. A photograph of (b) a typical pond and (c) a typical wallow.

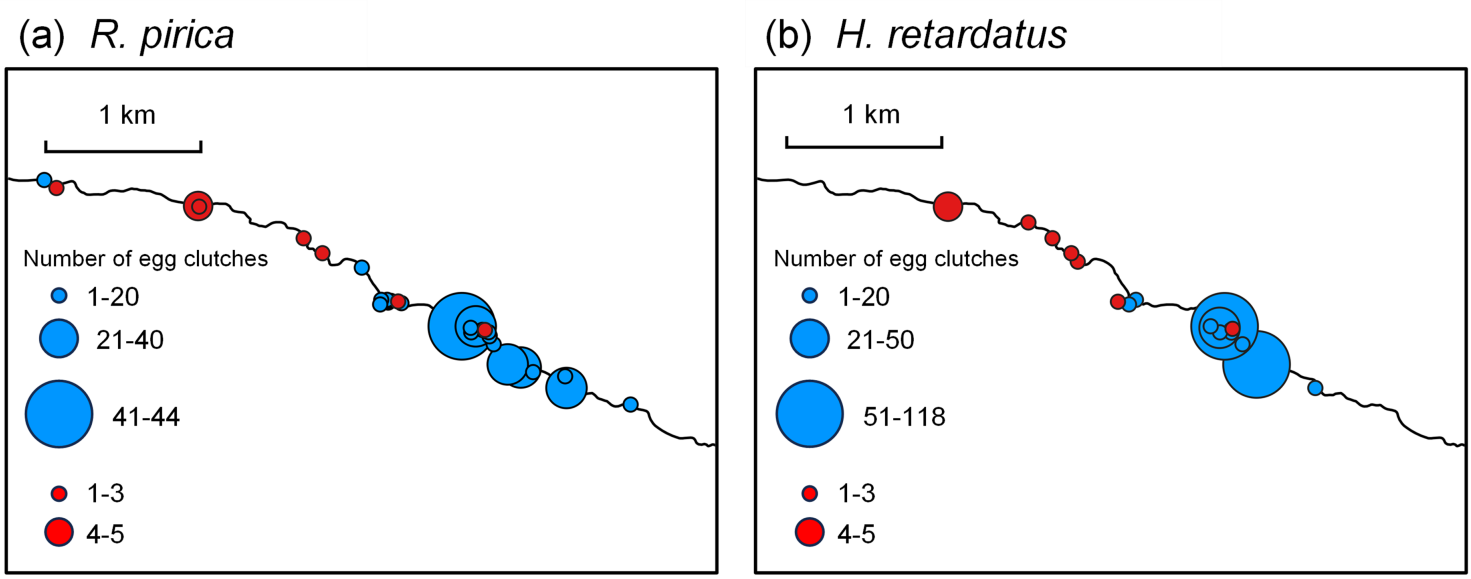


Figure 2

Oviposition sites and the number of egg clutches at each site for (a) *R. pirica* and (b) *H. retardatus*. The blue and red circles represent ponds and wallows, respectively. The size of circle represents the number of egg clutches, at a given site.

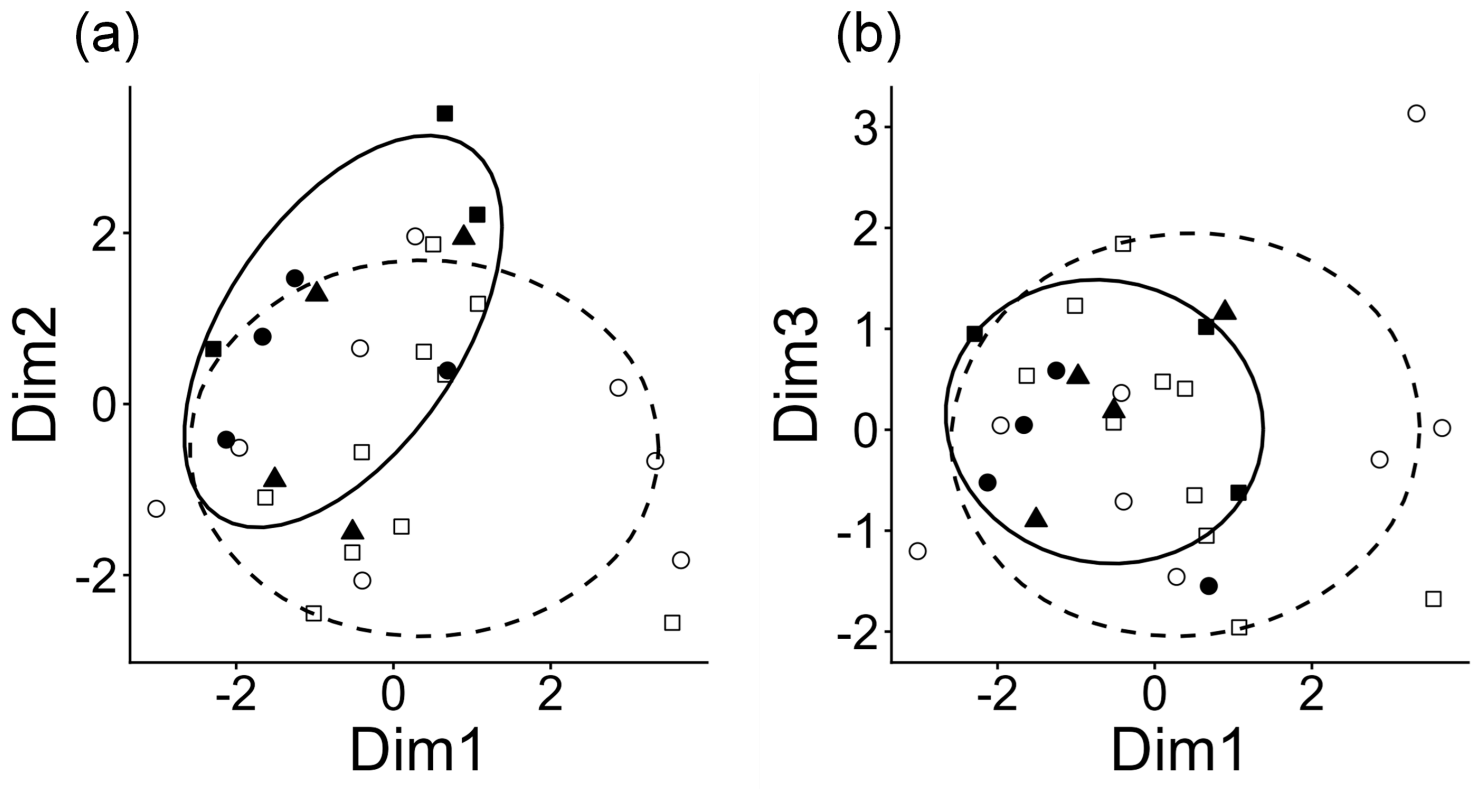


Figure 3

Environmental properties of ponds and wallows along the first three FAMD axes. Higher Dim1 scores are associated with higher pH and dissolved oxygen, larger water surface area, and greater stream connectivity. Higher Dim2 scores are associated with greater stream connectivity, spring presence, lower desiccation risk, shallower water, and higher electrical conductivity. Higher Dim3 scores are associated with higher dragonfly naiad density and water temperature. Circles indicate sites used only by *R. pirica*, triangles indicate sites used only by *H. retardatus*, and squares indicate sites used by both species. Ellipses indicate 68% concentration ellipses assuming bivariate normal distributions. Open symbols with dashed ellipses represent ponds, whereas filled symbols with solid ellipses represent wallows.

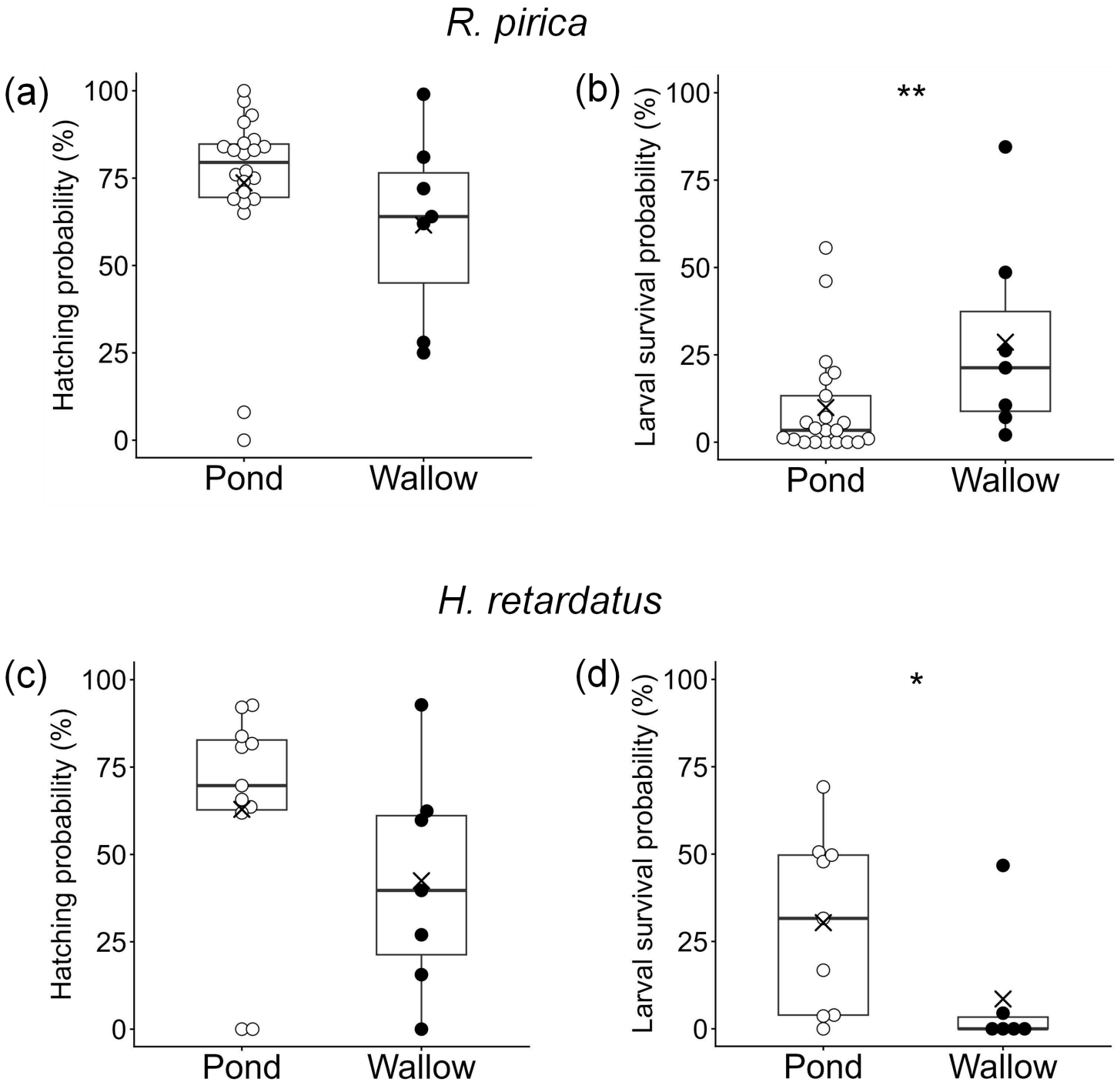


Figure 4

Survival probability of two amphibian species. Hatching probability of (a) *R. pirica* and (c)*H. retardatus*, and larval survival probability of (b) *R. pirica* and (d) *H. retardatus*. Boxes indicate medians and interquartile ranges, whiskers extend to 1.5 × IQR, and circles represent individual waterbodies. Crosses indicate mean values. Asterisks denote significant differences between ponds and wallows (* $P < 0.05$; ** $P < 0.01$).

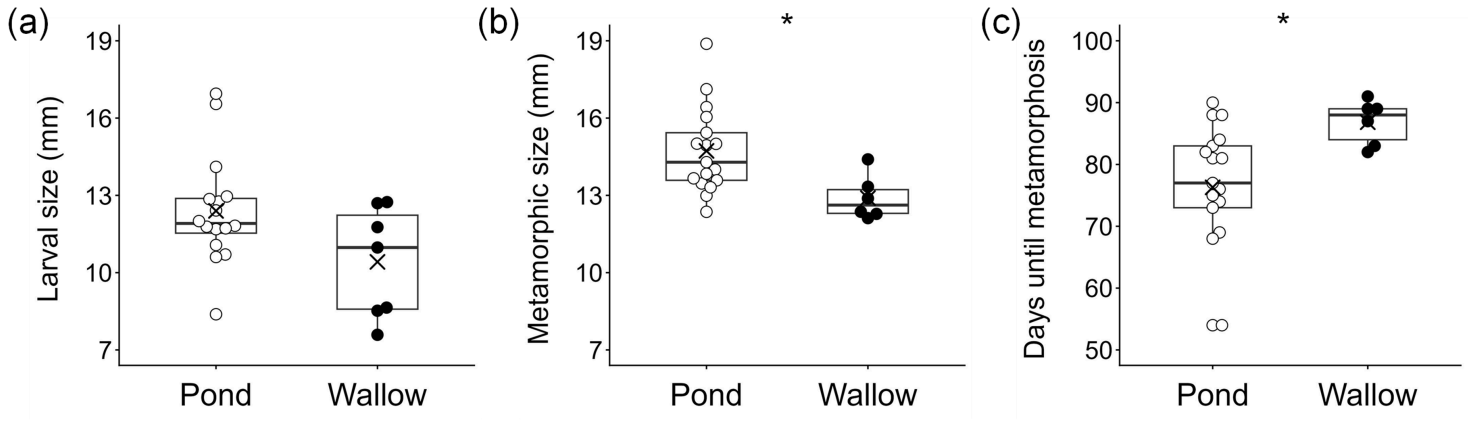


Figure 5

Size and time until metamorphosis of *R. pirica*: (a) Larval size (at middle larval stage: stage 25 or above [Gosner, 1960]), (b) Metamorphic size (stage 38 to 41 [Gosner, 1960]), (c) days until metamorphosis. Boxes indicate medians and interquartile ranges, whiskers extend to 1.5 × IQR, and circles represent individual waterbodies. Crosses indicate mean values. Asterisks denote significant differences between ponds and wallows (* $P < 0.05$).

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