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Demography and Morphometry of Fire-Bellied Toads in Two Contrasting Habitats in Obere Lobau, Vienna

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Abstract

This study investigates the population dynamics and morphometry of *Bombina bombina* in two ecologically contrasting habitats in the Obere Lobau (Vienna, Austria) over the period from 2016 to 2023. The aim was to assess the influence of habitat stability on demographic parameters, body size, body mass, and body condition. Demographic parameters were estimated from long-term capture–mark–recapture data using open population models, revealing clear differences between the two study sites. In the more stable habitat Seeschlacht, apparent survival was consistently higher, whereas per capita recruitment was substantially higher in the dynamic habitat Königshaufen. Population size was generally larger in Königshaufen but showed pronounced interannual fluctuations, while the population in Seeschlacht followed a more stable yet gradually declining trend. Individuals from Seeschlacht were significantly larger and heavier than those from Königshaufen. In contrast, body condition, measured using the scaled mass index (SMI), showed only minor differences between populations. The findings suggest that habitat stability is an important factor shaping demographic patterns and life-history traits in *Bombina bombina*. The dynamic habitat Königshaufen is characterized by high recruitment, lower survival, and increased investment into reproduction, whereas the stable habitat Seeschlacht is associated with higher survival rates and larger body size. These findings highlight the importance of maintaining hydrologically diverse floodplain habitats for the long-term conservation of fire-bellied toad populations.

Zusammenfassung

Die vorliegende Studie untersucht die Populationsdynamik und Morphometrie von *Bombina bombina* in zwei ökologisch kontrastierenden Habitaten der Oberen Lobau (Wien, Österreich) im Zeitraum von 2016 bis 2023. Ziel der Arbeit war es, den Einfluss der Habitatstabilität auf demographische Parameter, Körpergröße, Körpermasse und Körperkondition zu analysieren. Die demographischen Parameter wurden anhand langjähriger Fang-Wiederfang-Daten mithilfe offener Populationsmodelle geschätzt und zeigten deutliche Unterschiede zwischen den beiden Untersuchungsgebieten. Im stabileren Habitat Seeschlacht war die scheinbare Überlebensrate (apparent survival) durchgehend höher, während die Pro-Kopf-Rekrutierung im dynamischen Habitat Königshaufen deutlich höher war. Die Population im Königshaufen war insgesamt

größer, unterlag jedoch starken jährlichen Schwankungen, während die Population der Seeschlacht einem stabileren, jedoch langfristig rückläufigen Trend folgte. Die morphometrischen Analysen zeigten, dass Individuen aus der Seeschlacht signifikant größer und schwerer waren als jene aus dem Königshaufen. Im Gegensatz dazu unterschieden sich die Populationen hinsichtlich der Körperkondition, gemessen anhand des Scaled Mass Index (SMI), nur geringfügig. Die Ergebnisse deuten darauf hin, dass die Habitatstabilität ein wichtiger Faktor für die Ausprägung demographischer Muster und Life-History Traits bei *Bombina bombina* ist. Das dynamische Habitat Königshaufen ist durch hohe Rekrutierungsraten, geringere Überlebenswahrscheinlichkeiten und eine stärkere Investition in die Fortpflanzung gekennzeichnet, während das stabile Habitat Seeschlacht durch höheren Überlebensraten und größeren Körpermaße charakterisiert ist. Die Ergebnisse unterstreichen die Bedeutung hydrologisch vielfältiger Auenlebensräume für den langfristigen Erhalt von Rotbauchunkenpopulationen.

Keywords: *Bombina bombina; life-history strategies; population dynamics; habitat stability; morphometry; floodplain habitats*

Introduction

Amphibians are currently considered the most threatened vertebrate class globally, with approximately 41% of species threatened with extinction (Luedtke et al., 2023). The ongoing decline of amphibian populations is occurring at rates far exceeding natural background extinction rates (IPBES, 2019). Amphibians play an essential role as bioindicators due to their sensitivity to environmental changes, as they depend on both aquatic and terrestrial habitats throughout their life cycle (Wells 2007; Sparling et al., 2010). Habitat loss, degradation, fragmentation, climate change, pollution, invasive species, and emerging diseases pose severe threats to their survival (Hof et al., 2011; Luedtke et al., 2023). While habitat destruction remains the primary driver of amphibian population decline, the impact of climate change is becoming increasingly significant (Blaustein et al., 2010). Amphibians respond strongly to environmental fluctuations, which can influence traits such as body size, reproductive success, and survival (Hantzschmann et al. 2019; Cayuela et al., 2016b; Radchuk et al., 2019; Buckley et al., 2012). One species affected by these environmental pressures is the European fire-bellied toad (*Bombina bombina*), a small anuran distributed across

Central and Eastern Europe that reaches its westernmost distribution area in Austria (Glandt, 2015). *Bombina bombina* (Linnaeus, 1761) belongs to the order Anura, within the basal family Bombinatoridae and the genus *Bombina*. Adults typically reach a body length of approximately 4.5 to 5 cm, although smaller individuals are common. The weight lies between 2 and 14 grams (Gollmann et al., 2012). The dorsal surface is light to dark grey and covered with flattened warts. The ventral side is dark grey to black, featuring conspicuous orange to red blotches. This ventral colouration serves as an aposematic signal, warning potential predators of the toad's mildly toxic skin secretions and resulting unpalatability. *Bombina bombina* is the sister species of the yellow-bellied toad (*Bombina variegata*); where the distribution ranges of both species meet, hybridization occurs (Gollmann 1984). The yellow-bellied toad (*Bombina variegata*, Linnaeus 1758) is known for its relatively long lifespan, with individuals in the wild reportedly reaching up to 20 years of age (Gollmann et al., 2012; Płytycz and Bigaj 1993; Seidel 1993). Although *Bombina bombina* has a shorter lifespan, there are occasional reports of comparable longevity. Kinne et al. (2004) documented individuals living between 10 and 20 years in captivity, and similar lifespans have been observed under natural conditions as well (Gollmann et al., 2012). The age record in captivity is 29 years (Bannikov, 1969, as cited in Szczerbak and Szczerban 1980).

In Austria, *Bombina bombina* is primarily found in lowland regions in the eastern part of the country (Burgenland, Lower Austria, Vienna). Isolated records exist in the Danube wetlands of Upper Austria. Frequently used habitats are floodplains along river valleys in lowland areas. (Gollmann et al., 2012). Within the Lobau area, it is widely distributed. Although the species is well adapted to fluctuating environmental conditions, it remains strongly dependent on aquatic habitats throughout all stages of its life cycle. It prefers disturbance-dominated floodplain landscapes, such as sunny open meadows, forest edges, riparian zones, and reed beds in lowland areas. Breeding occurs in temporary, warm, sun-exposed, and structurally diverse water bodies (Pintar und Straka, 1990). Occasionally it uses shallow zones of larger, ideally fish-free, permanent standing waters with dense emergent and submerged vegetation, where egg clutches are deposited (Glandt et al., 2018; Günther and Schneeweiß 1996). The fire-bellied toad prefers clean and wind-sheltered breeding waters, where aquatic plants help reduce water movement caused by wind. In non-breeding habitats, the fire-bellied toad is less selective and also occupys water bodies of lower quality (Gollmann et al. 2012). With respect to waterbody size, *Bombina bombina* exhibits a eurytopic habitat preference (Vollmer und Große, 1999). However, more decisive for habitat

suitability are the presence of specific water depths and suitable shoreline profiles. In the most densely populated sites, shallow banks with an average water depth of approximately 50 cm (in spring) were predominant. Reproduction mainly occurred in shallow zones with depths of about 30–50 cm and moderate vegetation cover. Habitats with heavy shading, steep shorelines, and lacking shallow-water zones were entirely unsuitable (Engel, 1985, 1996; Günther und Schneeweiß, 1996; Wilkens, 1979). *Bombina bombina* avoids permanent water bodies due to increased predation pressure. Predators such as fish, leeches, dragonfly larvae, diving beetles, and their larvae reduce the survival chances of tadpoles in these habitats. Adult toads are preyed upon by various bird species, including storks, herons, and tawny owls, as well as by water shrews, adders and mammals such as badgers and polecats (Glandt et al. 2018; Semlitsch 2000; Wellborn et al. 1996). Habitat destruction and loss due to construction and drainage primarily threaten the fire-bellied toad, like all amphibian species. Herbicides and agrochemicals from agricultural practices, which enter the breeding waters, can also lead to developmental disorders and increased mortality (Plötner 2012; Gollmann 2007). *Bombina bombina* is a prolonged breeder. Reproductive conditions are highly dependent on weather and precipitation, to which *Bombina bombina* can respond with considerable flexibility. If conditions are suitable, the reproductive activity spans from early spring to late summer (Cabela et al., 2001; Gollmann et al., 2012).

Although *Bombina bombina* is not globally threatened (IUCN 2024), it is classified as Vulnerable (VU) on the Austrian Red List (Gollmann 2007) and is strictly protected under Annexes II and IV of the EU Habitats Directive. The primary threat to the species is habitat loss, particularly through the destruction, fragmentation, and degradation of suitable breeding sites.

The study area in the Donau-Auen National Park has undergone significant hydrological alterations since the river regulation measures of the 19th century. These interventions substantially modified the ecosystem, leading to a reduction of its former floodplain dynamics (Schratt-Ehrendorfer und Rotter 1999; Weigelhofer et al. 2013). Over the past century, more than 80% of the original floodplain areas along the Danube have been lost due to hydraulic engineering projects (Hein et al. 2014; Tockner and Stanford 2002). The Lobau has also been markedly influenced, with its hydrological regime undergoing profound transformation (Weigelhofer et al. 2013). Because of these regulatory measures, the Lobau was almost completely disconnected from the main channel of the Danube, interrupting natural sediment relocation processes and promoting siltation. This

development is particularly evident in the Obere Lobau, where water bodies are smaller and more susceptible to silting compared to the Untere Lobau (Reckendorfer et al. 2013). Despite declining groundwater levels and increasing desiccation, the Lobau still provides suitable habitat and breeding waters for *Bombina bombina*, due to the presence of remaining aquatic sites**.** Floodplain landscapes are highly dynamic, azonal habitats. In amphibian populations, recurring fluctuations in water levels are key factors that determine both the quality and availability of suitable habitats. When observed over multiple years, amphibian populations typically exhibit pronounced fluctuations in population size (Green 2009). These dynamics are primarily influenced by a combination of biotic and abiotic factors such as weather conditions, habitat quality, food availability, genetic diversity, environmental stressors and predation risk. Populations of species inhabiting unpredictable environmental conditions can differ in their status even when occurring in adjacent areas (Cogălniceanu and Miaud 2003; Philippi 2013). Environmental variability plays a key role in shaping life history, as it directly or indirectly impacts factors such as survival and recruitment. strategies (Tuljapurkar et al., 2009; Cayuela et al 2016b). The ontogenesis of amphibians follows a sequence of adaptive processes aimed at maximizing survival and reproductive success. Throughout their life cycle, energy and nutritional resources are distributed among growth, somatic maintenance, and reproductive investment (Pianka 1976). While growth and bodily maintenance support longevity, reproductive investment is directed toward offspring production. Fluctuating environmental conditions influence how energy is allocated at different developmental stages, acting as a selective pressure that shapes or constrains possible life history strategies. When environmental variability leads to high adult mortality, natural selection tends to favour early maturity and increased reproductive output, characteristics associated with "fast" life history strategies along the "slow–fast continuum" (Cayuela et al, 2016b; Tuljapurkar et al., 2009). Conversely, when fluctuations primarily impact birth rates and juvenile survival, selection promotes a longer lifespan, delayed maturity, and reduced reproductive investment, aligning with "slow" life history traits (Morris et al., 2008). Research by Cayuela et al. (2016b) demonstrated that environmental unpredictability influences the balance between survival and reproductive allocation in *Bombina variegata*, highlighting the role of ecological pressures in shaping life history trade-offs. Understanding amphibian population dynamics is vital for effective conservation efforts. Long-term studies are particularly valuable for identifying trends in population size, recruitment, survival, and body condition (Fujiwara and Takada, 2017). Capture-mark-recapture (CMR) studies provide important insights into these parameters, offering a robust method for

assessing population changes over time (Pollock, 2000; Amstrup et al., 2005; Huemer, 2023). The first capture–mark–recapture surveys on *Bombina bombina* were carried out in 2008 as part of field courses of the University of Vienna in of the Obere Lobau. The habitats of the two populations, Seeschlacht and Königshaufen, differ markedly in their environmental conditions. Seeschlacht is situated behind the Danube flood dike and is characterized by relatively stable water levels, whereas Königshaufen is located on the riverside of the dike and experiences a more dynamic hydrological regime with pronounced intra- and interannual fluctuations in water levels. (Philippi 2013, Huemer 2023). In the Seeschlacht area, adult toads dominated, while many juveniles and sub-adults were encountered in the larger population at Königshaufen. These contrasting population structures can be explained by greater reproductive success at Königshaufen and higher survival rates in Seeschlacht (Philippi und Gollmann, 2014; Huemer, 2023). This study aims to build upon the data previously analyzed by Huemer (2023) by incorporating the 2023 results. Furthermore, the extended dataset was analyzed morphometrically, focusing on length, mass, and body condition indices. The assessment of body condition has gained increasing attention in amphibian ecology, especially in the context of conservation efforts. Body condition, which can be defined as an animal's nutritional state or energy reserves, is often considered a measure or indicator of fitness and can provide insights into species declines and habitat requirements (Landler et al., 2022).

Hypotheses and Methodological Approach

Body Size and Mass between Populations

Due to the higher average age, the population of fire-bellied toads in the more stable habitat of Seeschlacht exhibits a larger body size and higher body mass than the population in the more dynamic habitat of Königshaufen.

Condition of Individuals

The individuals in the Königshaufen population have lower body condition than those in Seeschlacht. Due to the better reproductive conditions at Königshaufen, the toads invest more in reproduction there.

Material and Methods

Study Area

The Research was conducted in the Lobau, located in the eastern part of Vienna. This floodplain area covers approximately 22 km² (Czeike 1995). The majority of the area belongs to the city of Vienna, while a smaller section lies within Groß-Enzersdorf in Lower Austria. Since 1996, the Lobau has been part of the Donau-Auen National Park and, since 2004, also part of the European Natura 2000 network. The Viennese section was designated as both a Special Area of Conservation (SAC) and a Special Protection Area (SPA). River regulation measures have significantly altered this landscape since 1870 (Michlmayr 1997; Reckendorfer et al. 2013). The region has a continental sub-Pannonian climate, with annual precipitation ranging between 500 and 700 mm and an average annual temperature of approximately 10°C (Schiemer et al., 1999). Across the study years 2016 to 2023, annual precipitation ranged from 392.0 mm to 761.1 mm (mean across all eight years: 611.68 mm), annual mean temperature ranged from 10.9°C in 2021 to 12.1°C in 2018 (mean across all eight years: 11.47°C) (www.zamg.ac.at)

Table 1 Climate Data
Between 2016 and 2023, the region experienced the following climatic conditions:
Note: Climate data were obtained from a weather station in Groß-Enzersdorf (www.zamg.ac.at).

Year	Precipitation (mm)	Average Temperature (°C)
2016	692.5	11.2
2017	683.4	11.5
2018	392.0	12.1
2019	524.5	11.8
2020	666.2	11.4
2021	676.1	10.9
2022	497.6	11.3
2023	761.1	11.6

Following the construction of the Hubertus Dam on the left bank of the Danube in Vienna, large parts of the Lobau are no longer flooded during high water events. Although the dam greatly limits the natural dynamics of the area, the Danube water level still influences the groundwater level in the Lobau, leading to substantial fluctuations in water levels behind the dam. Water bodies primarily dry out in winter but also desiccate during prolonged heatwaves in summer (Philippi 2013). These fluctuations play a crucial role in shaping the hydrological conditions of the Lobau, influencing the availability of aquatic habitats and thus affecting the local amphibian populations

(Baart et al., 2013; Philippi and Gollmann, 2014). The gradual decline in groundwater levels and ongoing succession processes continue to alter the area's ecological structure, further emphasizing the importance of long-term ecological monitoring (Weigelhofer et al., 2005).

The Lobau is divided into two sections with distinct hydrological characteristics. Since the implementation of regulation measures in the 19th century, the hydrological system has been cut off from the effects of natural erosive flooding. Only the floodplain waters of the Untere Lobau remain directly connected to the Danube via the "Schönauer Schlitz" - a breach in the flood protection dike that allows occasional floodwaters to enter. As a result, the Untere Lobau is subject to significantly greater hydrological dynamics than the Obere Lobau (Reckendorfer und Hein 2006; Weigelhofer et al., 2011). The Obere Lobau is entirely disconnected from direct flooding events. Here, hydrological dynamics are primarily influenced by groundwater fluctuations, which determine the availability and persistence of aquatic habitats (Schiemer et al., 1999; Weigelhofer et al., 2013). To counteract the drying of the Obere Lobau and improve its hydrological conditions, a water enhancement scheme was initiated in the late 1990s. The aim was to re-establish controlled surface water connectivity and ensure minimum water levels in the Seeschlacht areas during the vegetation period (Imhof et al. 1992). Since 2001, this has involved a regulated surface water supply from the Alte and Neue Donau, diverted via the Oberes Mühlwasser into the Obere Lobau through a chain of backwaters (Funk et al. 2009). This newly established inflow gradually replaced the previously dominant groundwater supply (Weigelhofer et al. 2011; Reckendorfer and Hein 2006). The water is supplied only from March to October to allow for the natural drying of the floodplain during the winter (Funk et al. 2009). As a result, a moderate seasonal increase in water levels has been observed, positively influencing both the availability and temporal dynamics of aquatic habitats (Weigelhofer et al. 2013). In addition, a new water diversion system was established in 2023 via the Panozzalacke, where water from the Neue Donau is piped into the Panozzalacke and then flows through existing channels to other water bodies within the Obere Lobau (Stadt Wien, o. J.)

Study Sites

The data for this study were collected in the Obere Lobau in two areas, "Seeschlacht" and "Königshaufen" (Fig. 1), which are characterized by contrasting environmental conditions. The "Seeschlacht" area covers approximately 150,000 m² and is dotted with numerous bomb craters,

which today serve as biotopes for amphibians. Several of the resulting ponds are located within a seasonally flooded reed zone. Depending on the water level, these ponds are partially connected by narrow water channels. “Seeschlacht” is situated behind the Hubertus Dike, belongs to the section that receives Danube water inflow, and is therefore less dependent on the Danube’s water level than the “Königshaufen” area.

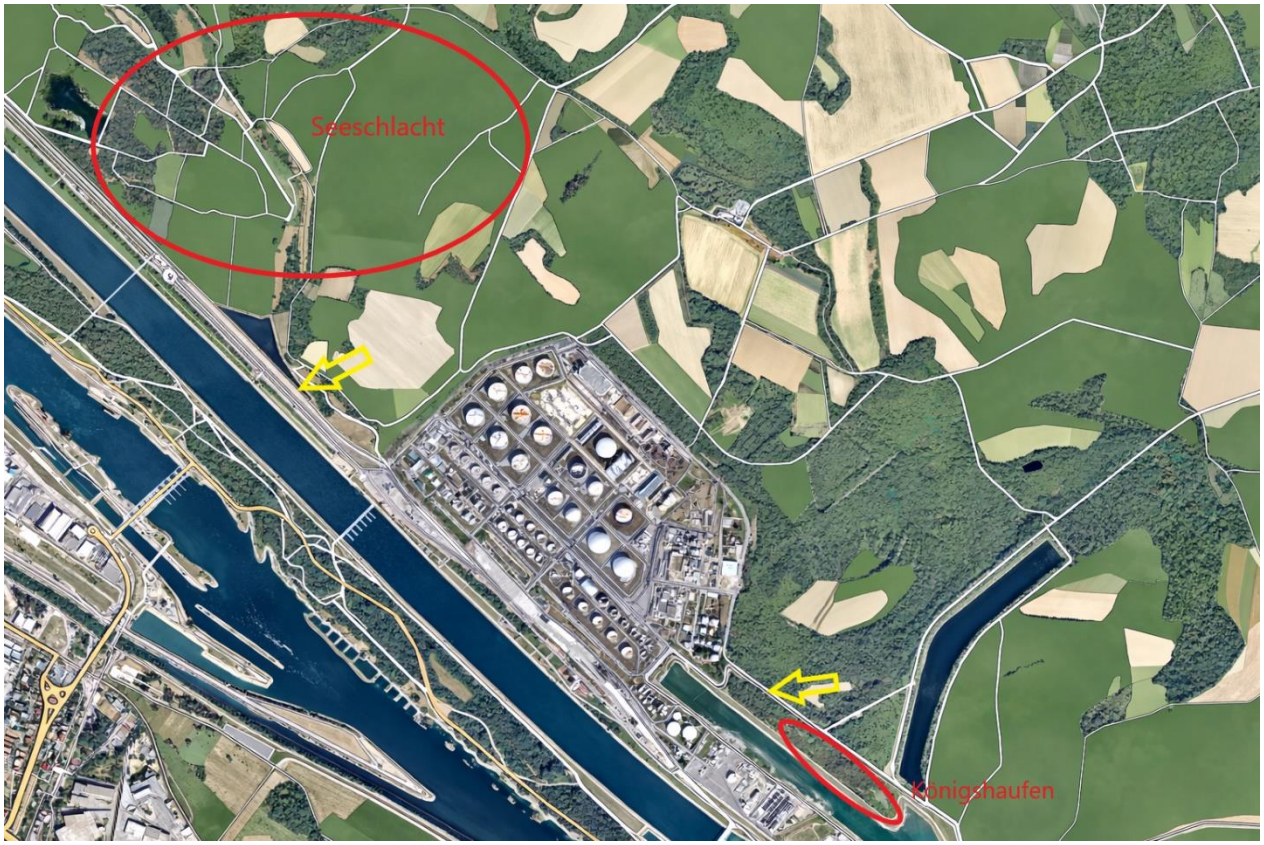

Fig. 1: Aerial view of the two spatially separated areas “Seeschlacht” and “Königshaufen”. The OMV tank farm is located between them. The arrows indicate the Hubertus Dike. The “Seeschlacht” area is situated behind the dike, whereas the two water bodies in the “Königshaufen” area lie in front of it. (Source: www.googlemaps.at) The map was created with QGIS (2026) (v3.30.0; www.qgis.org/).

The second site, “Königshaufen,” is located on the opposite side of the oil harbor in the southeast and consists of two semi-permanent water bodies situated approximately 25 meters apart. At average water levels, their surface areas are about 4,000–5,000 m² (“No. 62”) and 3,000–4,000 m² (“No. 63”), respectively. The surrounding vegetation is characteristic of softwood floodplain forest, dominated by white and crack willow (*Salix alba*, *Salix fragilis*) as well as black and white poplar (*Populus nigra*, *Populus alba*) (Lazowski and Mann 2000). At both study sites, the vegetation gradually transitions into hardwood floodplain forest, with tree species such as common ash (*Fraxinus excelsior*) and Norway maple (*Acer platanoides*).

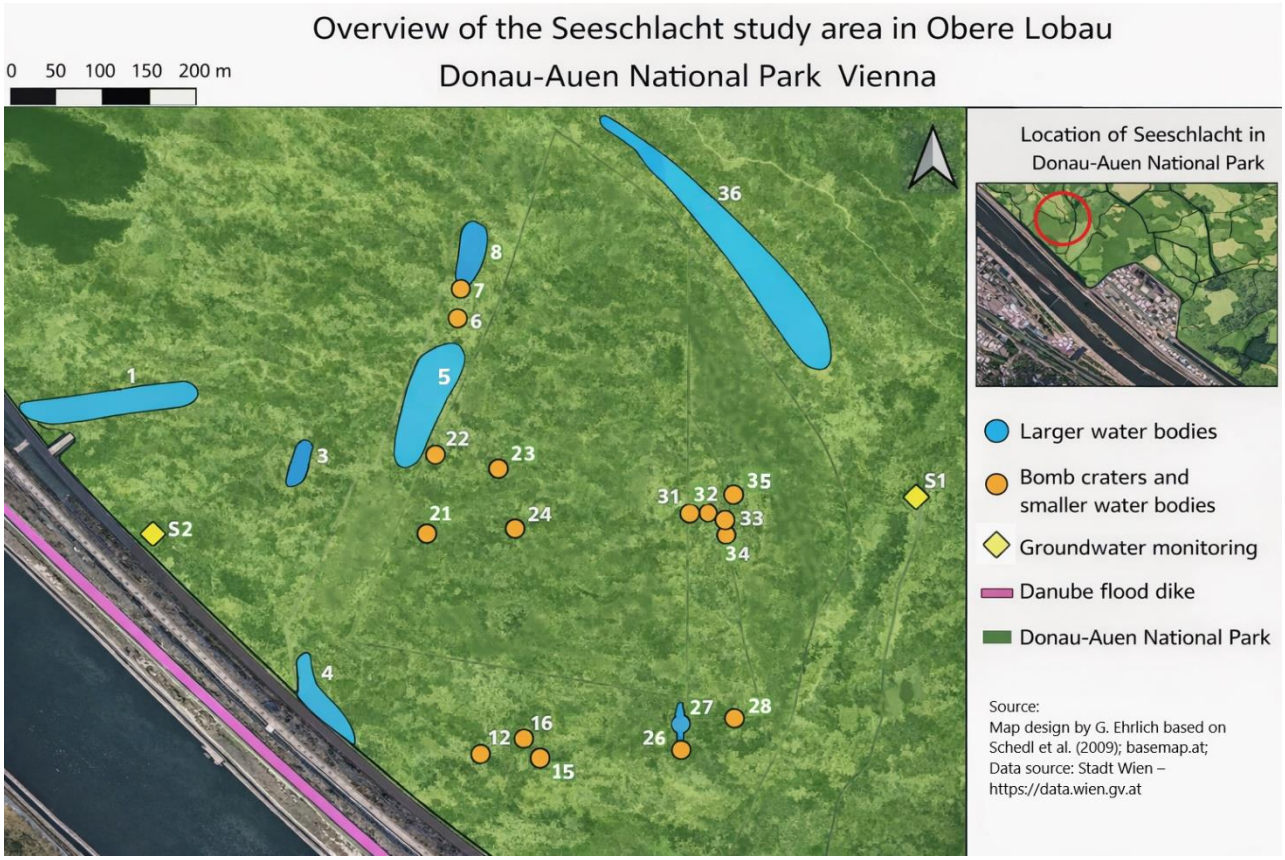

Fig. 2: Aereal view of the core study area in Seeschlacht. The figure is based on the schematic representation by H. Schedl et al. (2009). A selected part of the area was used for our investigation. The orange dots indicate bomb craters from 1944/45. The large orange zones represent permanent water bodies. The blue-shaded areas are meadows that are temporarily inundated but can also dry out (Source: www.googlemaps.at) The map was created with QGIS (2026) (v3.30.0; www.qgis.org/).

Water Bodies in the "Seeschlacht" Area

Large parts of the "Seeschlacht" area consist of open terrain without forest vegetation. In these sections, high solar radiation occurs at the beginning of the season. During the study period, the vegetation increased noticeably. In particular, reeds and grasses spread extensively, resulting in shading the ponds and water-filled channels. By July, the channels connecting individual ponds were in some places almost completely overgrown, which significantly hampered the capture and detection of fire-bellied toads (Figs. 3 and 4). Due to its location behind the Danube flood dike, Seeschlacht experiences relatively stable environmental conditions, with water levels remaining mostly constant or fluctuating only slightly. Consequently, this site is classified as "stable."

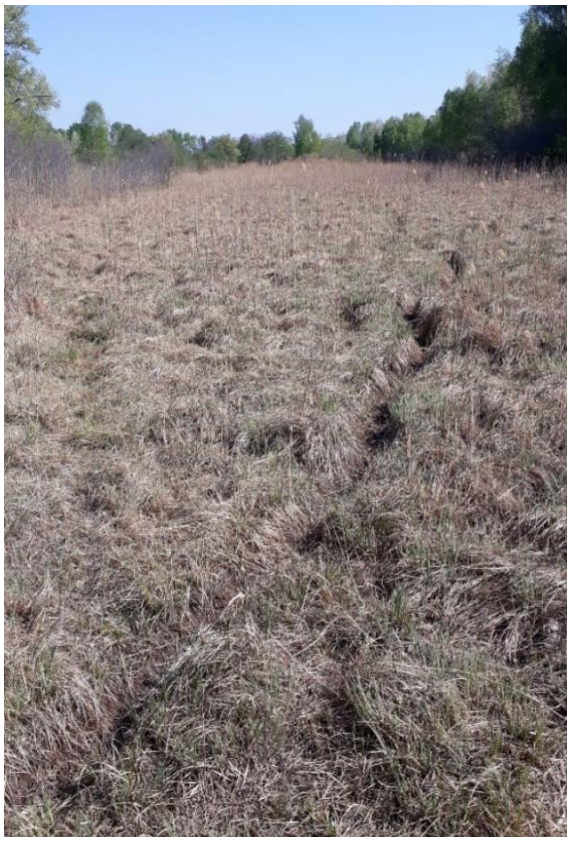

Fig. 3: Area 5 on April 29, 2022 – vegetation is still sparsely developed

Fig. 4: The same area on July 6, 2022 vegetation already partially covers the water filled channels

Some bomb craters that have formed ponds are located within forest vegetation, shaded by trees, cooler in temperature, and remain devoid of vegetation even later in the season (Fig. 5). Their water contains large amounts of deadwood and a higher concentration of humic substances. Primary production at these sites is low, and due to the absence of macrophytes, oxygen levels are also reduced. In some areas, these ponds are relatively deep and accumulate large quantities of dead organic matter, which is partially decomposed through anoxic processes, releasing methane. A change in light conditions would undoubtedly and fundamentally alter the character of such water bodies within a short period of time. Since fire-bellied toads prefer sun-exposed waters for reproduction, the shaded bomb craters do not serve as breeding sites.

Fig. 5: Bomb crater shadowed by trees

Other bomb craters are in partial shade and exhibit neither reed growth nor submerged aquatic plants. However, as the season progresses and day length increases with improved light conditions, duckweed can spread across these ponds, eventually covering the entire water surface (Fig. 6). Bomb craters exposed to full sunlight are entirely overgrown with reeds (Fig. 7).

Fig. 6: Bomb crater in partial shade

Fig. 7: Bomb crater exposed to full sunlight.

Water Bodies in the "Königshaufen" Area

The area known as the "Köngishaufen" consists of two shallow water bodies, labeled "62" and "63." At average water levels, both ponds are surrounded by trees right at the shoreline. Depending on the time of day, these trees shade different areas of the water surface. The ponds also contain large amounts of deadwood (Philippi 2013). Some trees have been slowly decomposing for decades. Since the ponds are located in front of the Hubertus Dam, their water level is strongly influenced by the water level of the Danube. Both ponds experience large shifts in water level during the year. As the ponds occasionally dry out completely, this area is characterized by fluctuating environmental conditions.

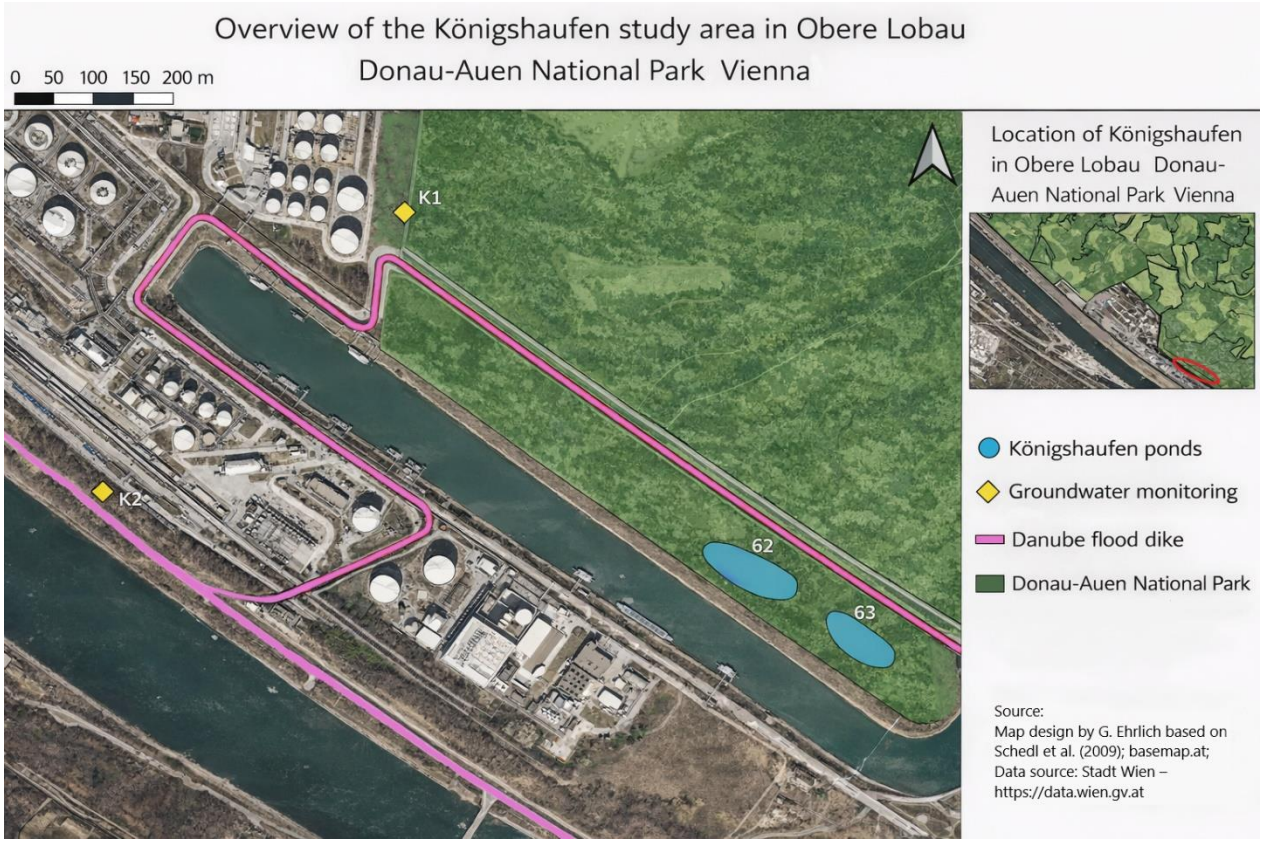

Fig. 8: Aereal view of the study area in Königshaufen. The two ponds (62 and 63) are situated on the riverside of the Danube flood protection dike and are directly affected by periodic fluctuations of the Danube River. The map was created with QGIS (2026) (v3.30.0; www.qgis.org/).

Fig. 9: Pond "62" on 23.03.2022, View towards the west. The dried-out pond contains extensive deposits of dead wood, which can retain substantial amounts of water and offer moist refuges for toads, even when the pond is empty.

Fig. 10: Pond "62" on 18.05.2022, front section. The water is shallow and warm, with rich structural features such as dead wood and aquatic vegetation.

Whenever the ponds hold water, they are successful breeding sites.

The firebellied toads (*Bombina bombina*) share their habitat with the Danube crested newt (*Triturus dobrogicus*), tree frogs (*Hyla arborea*), agile frogs (*Rana dalmatina*), water frogs (*Pelophylax esculentus* complex), and common spadefoot toads (*Pelobates fuscus*) (Gollmann 2016; Schedl et al. 2009). The structurally complex surrounding landscape provides numerous suitable refuges for hibernation.

Fig. 11: Pond 63 on 23.03.2022, almost dry

Fig. 12: Pond 63 on 13.04.2022 with high water level

Water levels can change significantly within a few weeks, creating unstable environmental conditions

Data Collection

Survey Period

The study sites, Königshaufen and Seeschlacht, were surveyed from 2016 to 2023 between March and August. Seeschlacht was visited a total of 43 times, Königshaufen was visited a total of 46 times (Table 2). Sampling of *Bombina bombina* began in the late morning and continued until the late afternoon.

Table 2: Number of sampling occasions per year in each study area

Year	Study site	Times visited
2016	Seeschlacht	5
	Königshaufen	5
2017	Seeschlacht	4
	Königshaufen	5
2018	Seeschlacht	5
	Königshaufen	6
2019	Seeschlacht	6
	Königshaufen	7
2020	Seeschlacht	5
	Königshaufen	4
2021	Seeschlacht	6
	Königshaufen	7
2022	Seeschlacht	7
	Königshaufen	7
2023	Seeschlacht	5
	Königshaufen	5
Total	Seeschlacht	**43**
	Königshaufen	**46**

Individual toads were captured by sight in shallow water, using a dip net or by hand, and were temporarily placed in a container with a small amount of water. To minimize stress and reduce the time spent in the collection boxes, the study area was sampled in sections.

Following capture, each individual was measured from the snout to the cloaca ("snout-vent length") using a plastic caliper with a precision of 0.1 mm. Due to the high flexibility of *Bombina bombina*, particular care was taken to position the specimens as straight as possible during measurement (Fig. 13).

Fig. 13: measurement of SVL with caliper

Fig. 14: weight measurement

Subsequent Measurements and Classification

Following the initial measurements, the toads were weighed using a digital scale (TUFF-WEIGHT 1000G X 0.1G) with a precision of 0.1 g (Fig. 14). Additionally, the unique ventral colour pattern of each toad was photographed using a digital camera to facilitate later identification of recaptured specimens. The abdominal pattern begins to develop shortly after metamorphosis but may still undergo changes during this early stage.

Age Classification

Individuals were categorized into three age classes. Toads with a snout-vent length (SVL) of at least 35 mm were classified as adults, indicating that they had survived at least two overwintering periods. Sex was determined for all adult individuals. Specimens measuring under 35 mm, presumably from the preceding breeding season, were classified as juveniles. In this group, sex determination was only possible if secondary sexual characteristics were already present or if behavioural cues, such as amplexus, provided indications of sex. Toads that had hatched in the current season and completed their metamorphosis were categorized as metamorphs.

Sex Determination

Sex determination in *Bombina bombina* requires a certain level of experience. Males were identified by the presence of dark nuptial pads on their forelimbs and fingers during breeding season (Nöllert und Nöllert, 1992). They also exhibit internal vocal sacs, which often leave visible skin folds on the throat in older or actively calling individuals (Philippi, 2013). Although vocalizations during handling (release calls) are typical for males, they cannot be used as an exclusive marker since females occasionally emit similar sounds. Release calls from females, however, are typically quieter (Gollmann et al., 2009). Data from recaptured individuals sometimes allowed for sex determination later in the season when secondary sexual characteristics became more pronounced. All toads were released unharmed at their capture site immediately after measurement.

Fig. 15: male with nuptial pads

Fig. 16: female withoud nuptial pads

Identification of Recaptures

Recaptured fire-bellied toads were identified using the software IBEIS (Image-Based Ecological Information System) (Crall 2021). This is an image-based recognition tool that analyzes characteristic patterns, in this case, the unique ventral colouration of each animal, by comparing photographs. IBEIS applies pattern recognition algorithms to match new images with an existing database, enabling the reliable identification and re-identification of individuals (Fig. 17 - 19).

Fig. 17: First capture on May 18, 2022 in Königshaufen

Fig 18: recapture of the same individual in Königshaufen on june 1, 2022

Fig. 19: *Identification of a recapture match using the IBEIS software. The density of the lines illustrates the extent of spatial alignment between the matched images*

Since IBEIS operates exclusively on Linux-based operating systems, the freely available software VirtualBox (2021) was used to run a virtual Linux environment on a Windows system. First, the images were manually cropped to standardize framing, ensuring that the full ventral pattern of each individual was visible while excluding unnecessary background. This step was performed digitally prior to further processing to improve comparability among images and to facilitate reliable pattern recognition. The processed images were then imported into a database and organized into so-called image sets according to sampling occasions (i.e., field survey dates). Subsequently, the data were

prepared by annotating each image. In this process, the entire image was defined as a single annotation, as the basis for the automated comparison. The photo-identification process was conducted using an automated pattern-matching algorithm implemented in the software IBEIS. Image pairs were compared based on their ventral pattern and ranked according to a calculated similarity score. Higher scores reflect a greater degree of correspondence between patterns, indicating a higher probability that two images represent the same individual. As automated matching is not error-free, all suggested matches were verified through visual inspection. As a rule of thumb, approximately twice as many image pairs were inspected as the number of images in the respective sampling occasion. For example, if a sampling occasion comprised 100 images, the first 200 ranked image pairs were manually reviewed (Huemer 2023). Confirmed matches were validated and marked accordingly, allowing the assignment of consistent individual IDs across different sampling occasions. To reduce the risk of overlooking less obvious matches, additional targeted comparisons were performed for images with no or low-scoring matches. This ensured that individuals with weaker pattern similarity or lower image quality were still reliably identified. Finally, an internal comparison within each sampling occasion was conducted to detect potential recaptures (double captures) within the same survey event. All individuals that could not be matched to previously identified animals were assigned new unique IDs following a standardized naming scheme. These IDs were subsequently integrated into the dataset and used for further analyses.

Groundwater Levels

To match groundwater levels to capture events, water level data were assigned based on the date of capture. Groundwater levels were available from several monitoring sites in the study area. For each habitat, the monitoring station providing the most complete dataset was selected. For Seeschlacht, data from sensor S2 (Wien 22, Br 22-17; HZB number: 313015) were used, while for Königshaufen, data from sensor K2 (Wien 22, Bl 22-242; HZB number: 350215) were applied. Other available monitoring sites were excluded due to incomplete temporal coverage, particularly in later years of the study period. Groundwater data were provided by the Bundesministerium für Land- und Forstwirtschaft, Regionen und Wasserwirtschaft (BML; www.ehyd.gv.at/) and the Magistratsabteilung 45 (MA 45; Wiener Gewässer).

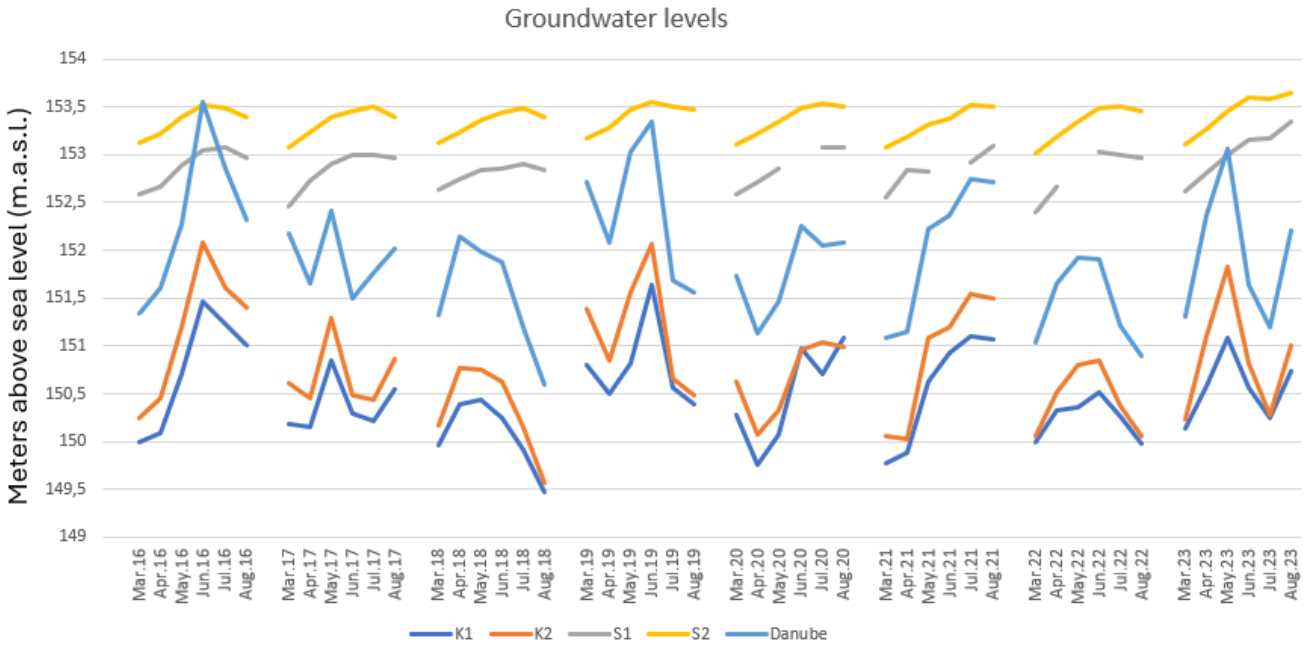

Fig. 20: Groundwater levels at monitoring sites K2 (Königshaufen) and S2 (Seeschlacht) from March to August across the study period. Values represent monthly mean groundwater levels. Data from additional monitoring sites (K1 and S1) were available for earlier years but were excluded from further analyses due to incomplete temporal coverage. Monthly mean water levels of the Danube recorded at the Donaukanalmündung monitoring station are also depicted in light blue.

Weather Data

Temperature and precipitation data were included as environmental covariates to assess their potential influence on morphometric traits and body condition. Data were obtained from the meteorological station Donaufeld, located in Vienna, Austria, and provided by GeoSphere Austria (https://data.hub.geosphere.at/). For each capture event, corresponding environmental conditions were assigned based on the date of capture. Monthly mean temperature (°C) and total monthly precipitation (mm) were used to allow comparability with groundwater data. These variables were included as fixed effects in the statistical models to evaluate their influence on body size (SVL), body mass, and scaled mass index (SMI).

Statistical Analysis

All statistical analyses were conducted using R (version 4.5.2; R Core Team, 2025). Population parameters were estimated using open population Jolly–Seber models implemented in the package *openCR* (Efford, 2025), allowing estimation of population size (N), apparent survival (φ), and

capture probability (p). Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AICc), and model averaging was applied where multiple models showed similar support (ΔAICc $\leq$ 2). The analyses were based on a robust design framework, with populations assumed to be closed within sampling periods and open between years. Morphometric relationships between body mass and snout–vent length (SVL) were analysed using log-transformed data to estimate the allometric scaling exponent (b), which was subsequently used to calculate the Scaled Mass Index (SMI) following Peig and Green (2009). The scaled mass index (SMI) was used as a proxy for body condition and energetic state. In contrast to simple mass-based or residual indices, the SMI accounts for the allometric relationship between body mass and body length, allowing comparisons of body condition independent of structural size. SMI calculation followed the standardized approach proposed Peig and Green (2009) using a reference body length and an allometric scaling exponent derived from the mass–length relationship. The scaling exponent was estimated using standardized major axis (SMA) regression implemented in the R package *smatr* (Warton et al., 2012a). To avoid pseudoreplication and ensure independence of data points, only one observation per individual (first capture) was included in the estimation of the scaling exponent.

Factors influencing body condition (SMI), body size (SVL), and body mass were analysed using linear mixed-effects models (LMMs), including individual identity as a random effect to account for repeated measurements. Fixed effects included habitat, year, day of year (DOY) as a proxy for seasonal variation, sex, and environmental variables. Environmental variables included groundwater level, temperature, and precipitation. Temperature and precipitation data were assigned to capture events based on the corresponding sampling month using the monthly mean temperature and total monthly precipitation values. Groundwater levels were obtained from the respective monitoring stations (S2 for Seeschlacht and K2 for Königshaufen) and matched to capture events on a monthly basis using mean monthly groundwater levels. Because groundwater levels differed substantially between study sites, groundwater values were centred within each site by subtracting the site-specific mean from each observation. This approach reduced multicollinearity between study site and groundwater levels and allowed the models to assess relative temporal fluctuations within sites rather than absolute differences between habitats. Model assumptions were assessed using diagnostic plots, including QQ plots and residual-versus-fitted plots, as well as variance inflation factors (VIF). Robust mixed-effects models were applied

where necessary to account for deviations from model assumptions and the presence of outliers. Data processing and visualisation were primarily performed using packages from the tidyverse framework, including *ggplot2* (Wickham et al., 2019). Mixed-effects models were fitted using the packages *lme4* (Bates et al., 2015), *nlme* (Pinheiro and Bates, 2000), and robustlmm (Koller, 2016). The scaling exponent for SMI calculation was estimated using *smatr* (Warton et al., 2012).

Capture Data

Capture–recapture data were compiled from field surveys, with individual identification based on photographic documentation of ventral patterns. To maintain data quality and consistency, several filtering steps were applied. Individuals without photographic records were excluded, as reliable identification was not possible. Duplicate capture events within the same sampling occasion were removed to avoid pseudoreplication, and metamorphs were excluded from all subsequent analyses due to their distinct morphology and uncertain classification. For morphometric analyses, only capture events with complete measurements of body mass and snout–vent length (SVL) were retained. Furthermore, for the calculation of the scaling exponent used in the Scaled Mass Index (SMI), only the first capture per individual was included to guarantee the independence of data points.

Results

A total of 6183 capture events were recorded over the entire study period (2016–2023). Following these filtering steps, 5715 capture events from 4519 identified individuals remained for further analyses. Of these capture events, 2583 involved adults (♂ = 1199; ♀ = 1384) and 3132 involved juveniles.

Table 3

Summary of capture data, recaptures, and age structure of Bombina bombina populations in Königshaufen and Seeschlacht between 2016 and 2023. Note: The total number of individuals refers to unique identified individuals across all study years and was not obtained by summing annual values. Recaptures refer to all repeated captures of previously identified individuals, regardless of whether the initial capture occurred in the same or in a previous year. Meta denotes the number of metamorph individuals per study year. These were excluded from the capture data.

Year	Study site	Individuals	Capture events	First time captures	Recaptures	Adults	Juveniles	Males	Females	Meta
2016	Königshaufen	451	466	451	15	145	321	74	71	9
2016	Seeschlacht	150	176	150	26	173	3	88	85	0
2017	Königshaufen	1153	1221	1121	100	280	941	152	128	1
2017	Seeschlacht	138	165	114	51	124	41	63	61	0
2018	Königshaufen	617	668	548	120	345	323	173	172	50
2018	Seeschlacht	152	189	91	98	160	29	77	83	0
2019	Königshaufen	292	344	235	111	286	58	101	185	64
2019	Seeschlacht	95	113	49	64	101	12	39	62	15
2020	Königshaufen	88	91	85	6	45	46	26	19	86
2020	Seeschlacht	102	125	79	46	60	65	24	36	0
2021	Königshaufen	421	462	416	46	48	414	25	23	66
2021	Seeschlacht	107	204	58	146	155	49	63	92	0
2022	Königshaufen	806	886	782	104	229	657	114	115	67
2022	Seeschlacht	108	207	43	164	185	22	71	114	2
2023	Königshaufen	262	278	235	43	160	118	72	88	77
2023	Seeschlacht	98	120	62	58	87	33	37	50	6
Total	Königshaufen	3873	4416	3873	545	1538	2,878	737	801	420
	Seeschlacht	646	1299	646	653	1045	254	462	583	23
	Total	4519	5715	4519	1198	2583	3132	1199	1384	443

Table 4 Capture Frequencies of fire-bellied toads.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Königshaufen	3411	398	52	9	2	0	1	0	0	0	0	0	0	0	0
Seeschlacht	398	114	47	29	18	12	8	8	1	5	2	1	2	0	1
Total	3809	512	99	38	20	12	9	8	1	5	2	1	2	0	1

Capture Frequencies and Recaptures

A total of 1198 capture events (21 % of all filtered capture events) were recaptures of previously identified individuals. Capture frequencies varied strongly among individuals, with most individuals being captured only once or a few times, and only a small proportion of individuals being captured repeatedly over multiple years. Individuals from Seeschlacht were recaptured more frequently and over longer periods than those from Königshaufen. Table 4 and Fig. 21 illustrate the distribution of capture frequencies across individuals and study sites.

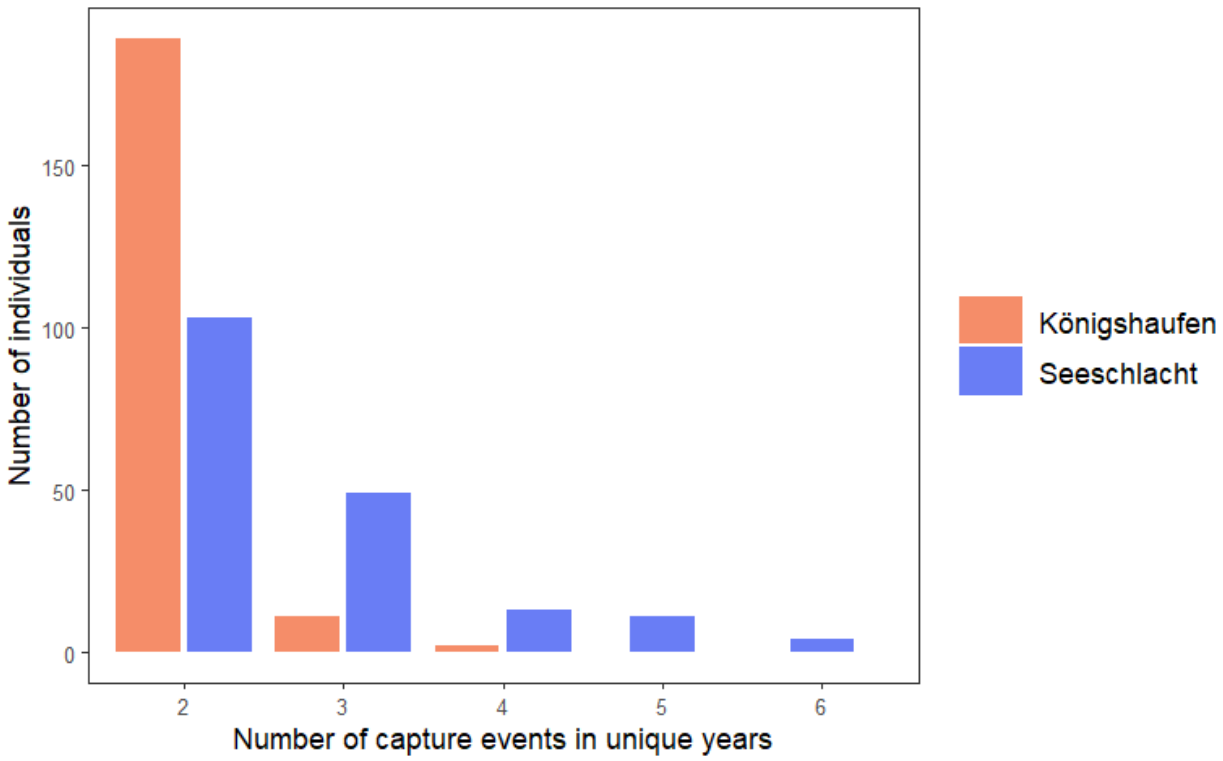

Fig. 21: Distribution of capture frequencies per individual across both study sites. Only captures across different years were considered; repeated captures within the same year were excluded from this representation.

Population Statistics

Model Type "JSSAfCL"

Population dynamics were analysed using Jolly–Seber–Schwarz–Arnason models with full conditional likelihood (JSSAfCL). Following the approach of Huemer (2023), models were fitted to the data and ranked according to their Akaike's Information Criterion corrected for small sample sizes (AICc) (Tables 5 and 6). Model averaging was applied to models within a ΔAICc < 2 to

account for model uncertainty. Only adult individuals were included in the analysis. For both study sites, models with time-dependent capture probability were among the best-supported. In Seeschlacht, the top-ranked models additionally included sex effects on capture probability and, in some cases, on demographic parameters, whereas in Königshaufen the best-supported model included time-dependent capture probability but constant apparent survival and recruitment.

Table 5
The 10 JSSAfCL Models with the lowest AICc for Königshaufen for adult individuals only

Number	model	npar	AICc	ΔAICc
1	p~t phi~1 f~1	10	13,292.28	0.00
2	p~t phi~sex f~1	11	13,292.31	0.03
3	p~t phi~1 f~sex	11	13,292.56	0.27
4	p~sex + t phi~1 f~1	11	13,292.85	0.57
5	p~sex + t phi~1 f~sex	12	13,293.12	0.84
6	p~sex + t phi~sex f~1	12	13,293.55	1.27
7	p~t phi~sex f~sex	12	13,294.56	2.28
8	p~sex + t phi~sex f~sex	13	13,295.39	3.10
9	p~1 phi~1 f~1	3	13,633.34	341.05
10	p~1 phi~sex f~1	4	13,633.37	341.09

Table 6
The 10 JSSAfCL Models with the lowest AICc for Seeschlacht for adult individuals only

Number	model	npar	AICc	ΔAICc
1	p~sex + t phi~1 f~1	11	8,637.53	0.00
2	p~sex + t phi~1 f~sex	12	8,637.86	0.33
3	p~sex + t phi~sex f~sex	13	8,638.15	0.62
4	p~sex + t phi~sex f~1	12	8,639.73	2.20
5	p~t phi~1 f~1	10	8,642.00	4.47
6	p~t phi~1 f~sex	11	8,643.67	6.14
7	p~t phi~sex f~1	11	8,644.18	6.65

Number	model	npar	AICc	ΔAICc
8	p~t phi~sex f~sex	12	8,645.38	7.85
9	p~sex phi~1 f~1	4	8,712.77	75.24
10	p~sex phi~sex f~sex	6	8,712.92	75.39

Capture Probability (p)

Capture probability (*p*) varied across years and between study sites, with values markedly higher in Seeschlacht compared to Königshaufen (Tables 7 and 8; Figs. 21 and 22). Differences between sexes were also evident, although small compared to the pronounced variation between sites. While JSSAfCL model estimates are shown here for this adult-only demographic analysis, JSSAN estimates for the total population size are reported separately in the context of population size estimation including juveniles.

Table 7
Capture probabilities for Königshaufen across the study years. Estimated using the averaged models. Note: p is the capture probability, SE denotes Standard errors, LCL the lower confidence limit and UCL the upper confidence limits for the 95% Confidence interval

	Female				Male			
year	p	SE	LCL	UCL	p	SE	LCL	UCL
2016	0.0108	0.0018	0.0079	0.0149	0.0101	0.0017	0.0073	0.0140
2017	0.0246	0.0033	0.0190	0.0318	0.0229	0.0031	0.0176	0.0298
2018	0.0319	0.0037	0.0254	0.0400	0.0297	0.0036	0.0234	0.0377
2019	0.0205	0.0023	0.0164	0.0256	0.0191	0.0024	0.0149	0.0244
2020	0.0061	0.0011	0.0043	0.0088	0.0057	0.0011	0.0039	0.0083
2021	0.0041	0.0008	0.0028	0.0059	0.0038	0.0007	0.0026	0.0056
2022	0.0170	0.0026	0.0126	0.0230	0.0159	0.0026	0.0115	0.0218
2023	0.0166	0.0030	0.0116	0.0237	0.0154	0.0030	0.0106	0.0225

Table 8
Capture probabilities for Seeschlacht across the study years. Estimated using the averaged models. Note: p is the capture probability, SE denotes Standard errors, LCL the lower confidence limit and UCL the upper confidence limits for the 95% Confidence interval

	Female				Male			
year	p	SE	LCL	UCL	p	SE	LCL	UCL
2016	0.0621	0.0072	0.0494	0.0779	0.0480	0.0058	0.0378	0.0607
2017	0.0595	0.0069	0.0473	0.0745	0.0459	0.0056	0.0361	0.0582
2018	0.0698	0.0071	0.0572	0.0850	0.0540	0.0060	0.0435	0.0670
2019	0.0402	0.0048	0.0318	0.0507	0.0309	0.0039	0.0240	0.0396
2020	0.0531	0.0077	0.0398	0.0704	0.0409	0.0063	0.0302	0.0551
2021	0.1155	0.0116	0.0945	0.1403	0.0903	0.0101	0.0724	0.1122
2022	0.1158	0.0104	0.0968	0.1378	0.0906	0.0092	0.0742	0.1102
2023	0.0967	0.0123	0.0752	0.1236	0.0753	0.0102	0.0576	0.0980

In Königshaufen, capture probabilities were similar between males and females across most years, with slightly higher values observed for females. Capture probability increased from 2016 to 2018, declined towards 2020–2021, and increased again in the later years (Fig. 22).

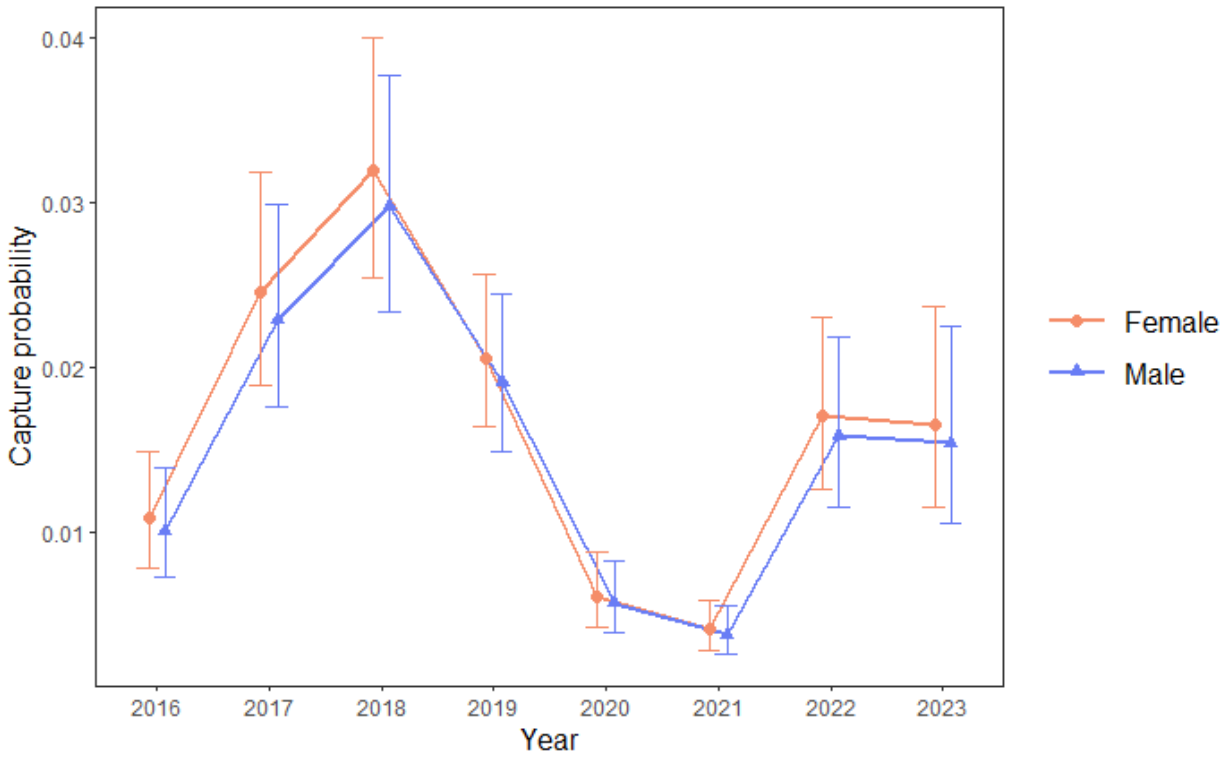

Figure 22
Capture probabilities for Königshaufen across the study years. Estimated using the averaged models
Note: the error bars show the upper and lower confidence limits for the 95% Confidence interval as estimated by OpenCR (N=2583 adult captures).

At all sampling occasions, capture probabilities were higher in Seeschlacht than in Königshaufen and followed a similar temporal pattern. Values increased from 2016 to 2018, declined around 2019–2020, and reached their highest levels in 2021–2022 before slightly decreasing again (Fig. 23).

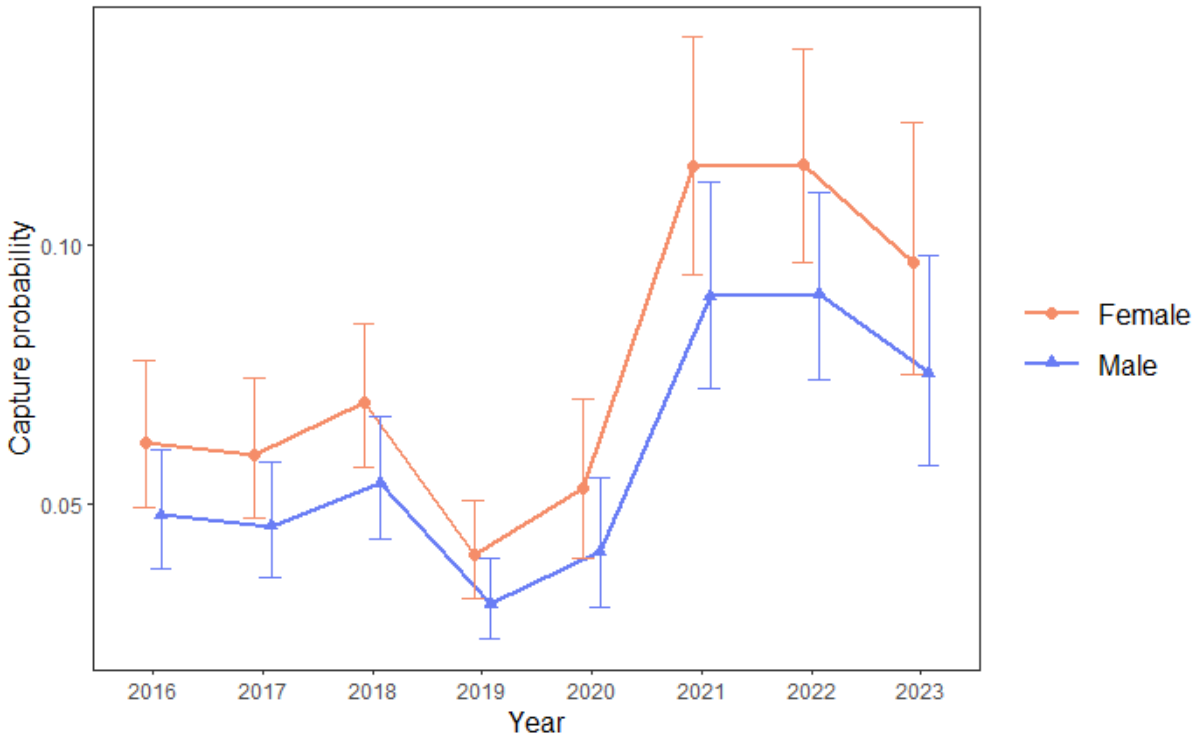

Fig. 23:
Capture probabilities for Seeschlacht across the study years. Estimated using the averaged models.
Note: the error bars show the upper and lower confidence limits for the 95% Confidence interval as estimated by OpenCR. (N=2583 adult captures)

Apparent survival (φ)

Apparent survival differed between study sites but showed only minor differences between sexes. At both sites, survival estimates were similar for males and females (Table 9). Across the study sites, apparent survival was in all study years higher in Seeschlacht than in Königshaufen, with markedly higher values observed in Seeschlacht (Fig. 24).

Table 9
Estimated annual apparent survival for both the averaged models for adult toads only.
Note: φ is the estimated apparent survival of each individual, LCL the lower confidence limit and UCL the upper confidence limits for the 95% Confidence interval

	Female			Male		
	φ	LCL	UCL	*φ*	LCL	UCL
Königshafen	0.3420	0.2829	0.4064	0.3324	0.2731	0.3975
Seeschlacht	0.5878	0.5415	0.6326	0.6023	0.5534	0.6493

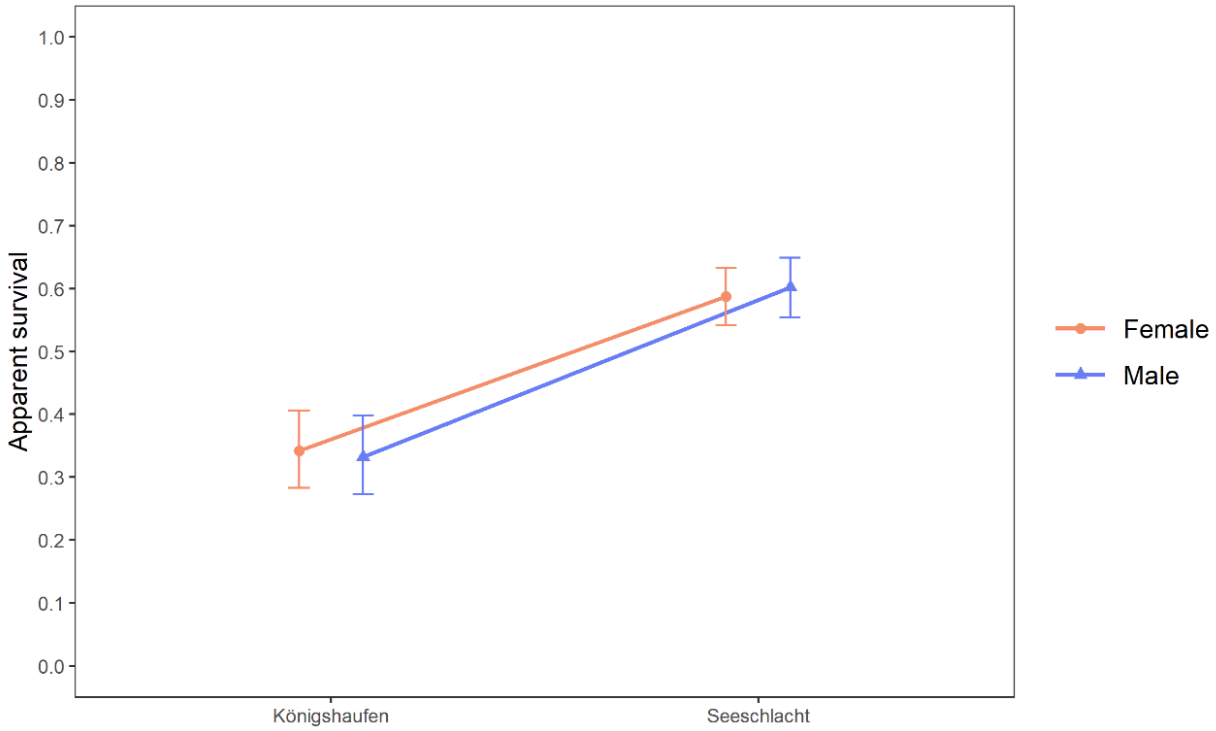

Fig. 24:
Apparent Survival of individuals for both sites. Estimated using the averaged models for adults only.
Note: the error bars show the upper and lower confidence limits for the 95% Confidence interval as estimated by OpenCR (N=2583 adult captures).

Per capita recruitment (f)

Per capita recruitment differed between study sites but showed only minor differences between sexes. In both populations, recruitment estimates were similar for males and females (Table 10). Across study sites, recruitment was higher in Königshaufen than in Seeschlacht, with substantially higher values observed in Königshaufen (Fig. 25).

Table 10
Estimated Per capita Recruitment for the averaged models for adult toads.
Note: f is the estimated per capita recruitment, LCL the lower confidence limit and UCL the upper confidence limits for the 95% Confidence interval.

	Female			Male		
	f	LCL	UCL	***f***	LCL	UCL
Königshafen	0.6221	0.5459	0.709	0.6118	0.5355	0.699
Seeschlacht	0.2651	0.2169	0.3241	0.2324	0.1821	0.2966

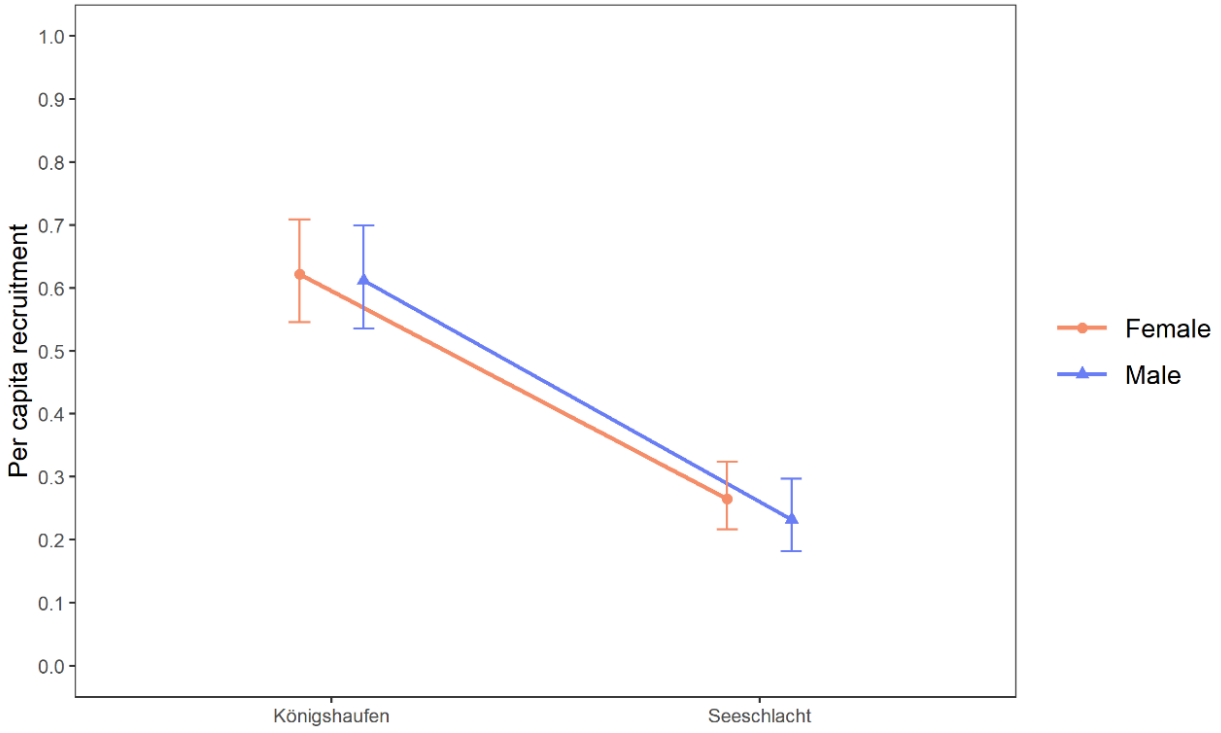

Fig. 25:
Per capita Recruitment for both sites. Estimated using the averaged models.
Note: the error bars show the upper and lower confidence limits for the 95% Confidence interval as estimated by OpenCR (N=2583 adult captures).

Model Type JSSAN

For the estimation of population size, Jolly–Seber models (JSSAN) were applied. Following the approach of Huemer (2023), models were ranked using Akaike's Information Criterion (AICc), and model averaging was performed for all models with ΔAICc < 2. Adult and juvenile capture events were included in the analyses (N = 5715). For Königshaufen, the models $p \sim sex + t$, $\varphi \sim 1$, $N \sim t$ and $p \sim sex + t$, $\varphi \sim sex$, $N \sim t$ were retained for model averaging. For Seeschlacht, the model $p \sim sex + t$, $\varphi \sim sex$, $N \sim t$ showed the strongest support (Tables 11 and 12). In both study sites, models including time-dependent variation in population size ($N \sim t$) were among the best-supported models.

Table 11
The 10 JSSAN Models with the lowest AICc for Königshaufen

Number	model	npar	AICc	ΔAICc
1	p~sex + t phi~1 N~t	19	37,934.78	0.00
2	p~sex + t phi~sex N~t	21	37,936.31	1.53
3	p~t phi~sex N~t	19	37,944.79	10.01
4	p~t phi~1 N~t	17	37,958.58	23.80
5	p~1 phi~sex N~t	12	37,994.58	59.80
6	p~sex phi~sex N~t	14	37,997.18	62.40
7	p~sex phi~1 N~t	12	38,000.76	65.98
8	p~1 phi~1 N~t	10	38,002.39	67.61
9	p~sex + t phi~sex N~1	14	38,148.32	213.54
10	p~sex + t phi~1 N~1	12	38,149.86	215.08

Table 12
The 10 JSSAN Models with the lowest AICc for Seeschlacht

Number	model	npar	AICc	ΔAICc
1	p~sex + t phi~sex N~t	21	10,672.70	0.00
2	p~t phi~sex N~t	19	10,687.75	15.05
3	p~sex + t phi~1 N~t	19	10,701.58	28.88
4	p~t phi~1 N~t	17	10,705.24	32.54
5	p~sex phi~sex N~t	14	10,750.50	77.80
6	p~sex + t phi~sex N~1	14	10,780.02	107.32
7	p~sex phi~1 N~t	12	10,780.96	108.26
8	p~1 phi~sex N~t	12	10,791.42	118.73
9	p~1 phi~1 N~t	10	10,803.17	130.48
10	p~t phi~sex N~1	12	10,803.99	131.29

For Königshaufen, two models showed similar support (ΔAICc < 2), and model averaging was applied to account for model uncertainty. Both models included time-dependent variation in population size ($N \sim t$) and sex- and time-dependent variation in capture probability ($p \sim sex + t$), while survival was modelled either as constant ($\varphi \sim 1$) or sex-dependent ($\varphi \sim sex$). In contrast, for Seeschlacht, a single model ($p \sim sex + t$, $\varphi \sim sex$, $N \sim t$) received substantially stronger support than all alternative models and was therefore retained as the best-supported model.

Capture Probability JSSAN

Estimated capture probabilities from the JSSAN models varied considerably among years, study sites, and demographic groups (Tables 13–14; Figs. 26–27). Capture probabilities were consistently higher in Seeschlacht than in Königshaufen across all years and demographic groups. In both study sites, juveniles generally showed the highest capture probabilities, whereas adult males tend to have the lowest values. Female capture probabilities were typically intermediate between males and juveniles.

Table 13
Capture probabilities for Königshaufen across the study years. Estimated by the averaged "p~sex + t phi~1 N~t" and "p~sex + t phi~sex N~t" JSSAN type models. Note: p is the capture probability, SE denotes Standard errors, LCL the lower confidence limit and UCL the upper confidence limits for the 95% Confidence interval

	Female				Male				Juvenile			
	p	SE	LCL	UCL	p	SE	LCL	UCL	p	SE	LCL	UCL
2016	0.0053	0.0016	0.0029	0.0094	0.0051	0.0015	0.0029	0.0089	0.0095	0.0024	0.0058	0.0157
2017	0.0115	0.0022	0.0079	0.0166	0.0110	0.0020	0.0078	0.0156	0.0207	0.0021	0.0170	0.0251
2018	0.0169	0.0026	0.0124	0.0229	0.0162	0.0024	0.0121	0.0218	0.0303	0.0035	0.0241	0.0379
2019	0.0305	0.0041	0.0234	0.0397	0.0294	0.0045	0.0218	0.0395	0.0542	0.0090	0.0391	0.0748
2020	0.0044	0.0019	0.0019	0.0102	0.0042	0.0018	0.0018	0.0097	0.0079	0.0034	0.0034	0.0183
2021	0.0104	0.0023	0.0067	0.0161	0.0100	0.0022	0.0065	0.0152	0.0187	0.0027	0.0140	0.0249
2022	0.0104	0.0019	0.0072	0.0150	0.0100	0.0018	0.0071	0.0142	0.0188	0.0019	0.0154	0.0229
2023	0.0106	0.0021	0.0072	0.0156	0.0102	0.0020	0.0069	0.0150	0.0191	0.0034	0.0135	0.0271

Table 14
Capture probabilities for Seeschlacht across the study years. Estimated by the "p~sex + t phi~sex N~t" JSSAN model. Note: p is the capture probability, SE denotes Standard errors, LCL the lower confidence limit and UCL the upper confidence limits for the 95% Confidence interval

	Female				Male				Juvenile			
	p	SE	LCL	UCL	p	SE	LCL	UCL	p	SE	LCL	UCL
2016	0.0578	0.0109	0.0398	0.0832	0.0456	0.0087	0.0313	0.0659	0.0761	0.0165	0.0495	0.1154
2017	0.0524	0.0077	0.0392	0.0698	0.0412	0.0062	0.0306	0.0554	0.0691	0.0108	0.0507	0.0936
2018	0.0656	0.0073	0.0526	0.0816	0.0518	0.0063	0.0408	0.0657	0.0862	0.0109	0.0672	0.1100
2019	0.0370	0.0051	0.0282	0.0485	0.0290	0.0043	0.0217	0.0387	0.0491	0.0077	0.0360	0.0665
2020	0.0520	0.0085	0.0376	0.0714	0.0409	0.0071	0.0291	0.0573	0.0686	0.0104	0.0508	0.0919
2021	0.1195	0.0119	0.0982	0.1448	0.0956	0.0109	0.0762	0.1192	0.1542	0.0144	0.1280	0.1846
2022	0.1071	0.0102	0.0886	0.1288	0.0853	0.0091	0.0691	0.1050	0.1387	0.0128	0.1154	0.1657
2023	0.0695	0.0103	0.0519	0.0925	0.0549	0.0085	0.0404	0.0742	0.0912	0.0129	0.0688	0.1198

At Königshaufen, capture probabilities remained comparatively low throughout the study period (Fig. 26). Probabilities gradually increased from 2016 onwards and reached a pronounced peak in 2019 for all demographic groups, particularly for juveniles. In 2020, capture probabilities declined strongly and remained low during the following years.

In Seeschlacht, capture probabilities were substantially higher and showed stronger interannual variation (Fig. 27). Capture probabilities were lowest in 2019 and increased markedly in 2021 and 2022, when all demographic groups reached their highest estimated values. Juveniles generally showed the highest probabilities, males the lowest values across most years.

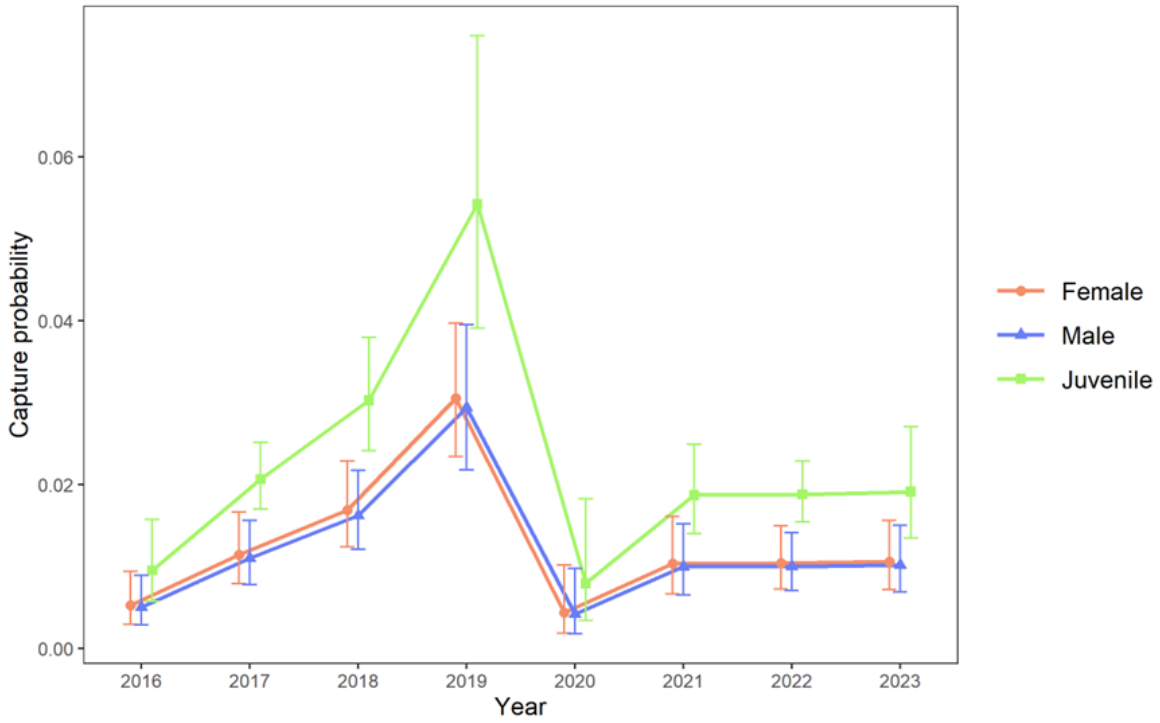

Figure 26
Capture probabilities for Königshaufen across the study years. Estimated by the averaged JSSAN type models. Note: the error bars show the upper and lower confidence limits for the 95% Confidence interval as estimated by OpenCR. Adult and Juvenile capture events were used for the models (N=5715).

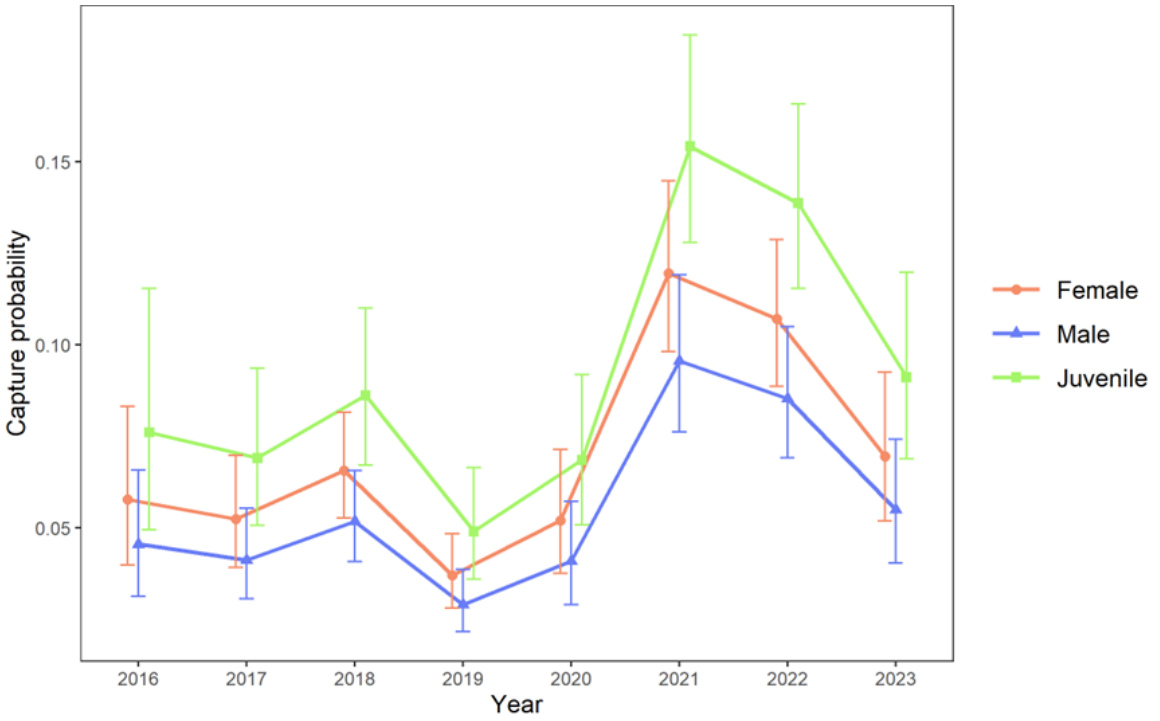

Fig. 27
Capture probabilities for Seeschlacht across the study years. Estimated by the "p~sex + t phi~sex N~t" JSSAN model Note: the error bars show the upper and lower confidence limits for the 95% Confidence interval as estimated by OpenCR. Adult and Juvenile capture events were used for the models (N=5715).

Population size (N)

Population sizes were estimated separately for each study site using Jolly–Seber models (JSSAN). Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AICc). Annual population estimates were obtained either from the best-supported models or from model-averaged estimates where applicable (Table 15). The resulting estimates varied substantially across years (Table 15; Figs. 28–29). Throughout the study period, population sizes were consistently higher in Königshaufen than in Seeschlacht

Table 15
Population sizes estimated by the averaged JSSAN models for both sites across the study years. Note: estimates wererounded to the nearest integer value. LCL the lower confidence limit and UCL the upper confidence limits for the 95% Confidence interval

	Königshaufen			Seeschlacht		
Year	N	LCL	UCL	N	LCL	UCL
2016	6701	4050	11087	418	297	588
2017	9100	7233	11450	470	365	605
2018	3115	2585	3755	327	270	396
2019	785	641	962	265	212	332
2020	1789	818	3911	347	265	454
2021	2995	2188	4100	175	147	209
2022	4812	3861	5997	147	123	177
2023	2009	1489	2711	221	174	281

At Königshaufen, population size showed pronounced interannual fluctuations (Fig. 28). Estimates increased significantly during the first years of the study, peaking in 2017 at approximately 9100 individuals. After a marked decline between 2017 and 2019, the population recovered until 2022 before declining once more in 2023. Confidence intervals tended to be broader in Königshaufen than in Seeschlacht, indicating lower precision of the annual estimates, likely related to stronger temporal fluctuations and variation in capture probabilities.

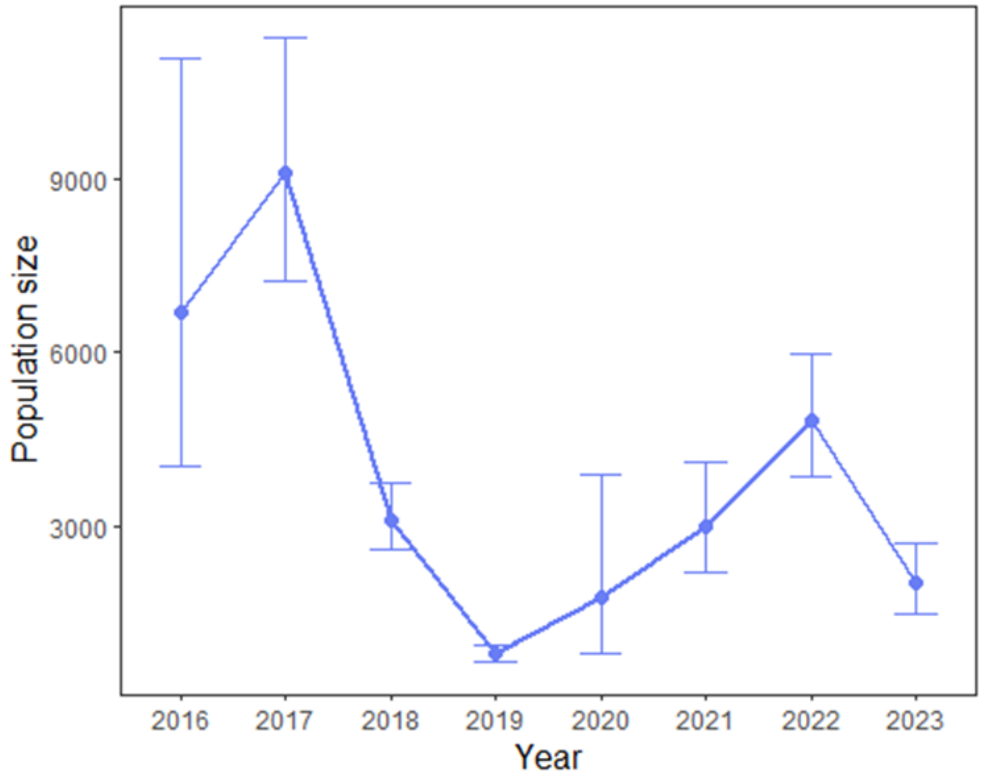

Fig. 28:
Estimated population sizes for Königshaufen across the study years. Estimated by the "p~t phi~1 N~t" JSSAN type model. Note: the error bars show the upper and lower confidence limits for the 95% Confidence interval as estimated by OpenCR. Adult and Juvenile capture events were used for the models (N=5715).

In Seeschlacht, population size was considerably lower and showed a more gradual temporal pattern. Following a peak in 2017 (N = 470), population size declined over the study period and reached its minimum in 2022 (N = 147). Although some short-term fluctuations occurred, particularly in 2020 and 2023, the overall trend indicated a long-term decrease in population size. The fitted regression line (Fig. 29) further illustrates this declining trend across the study years.

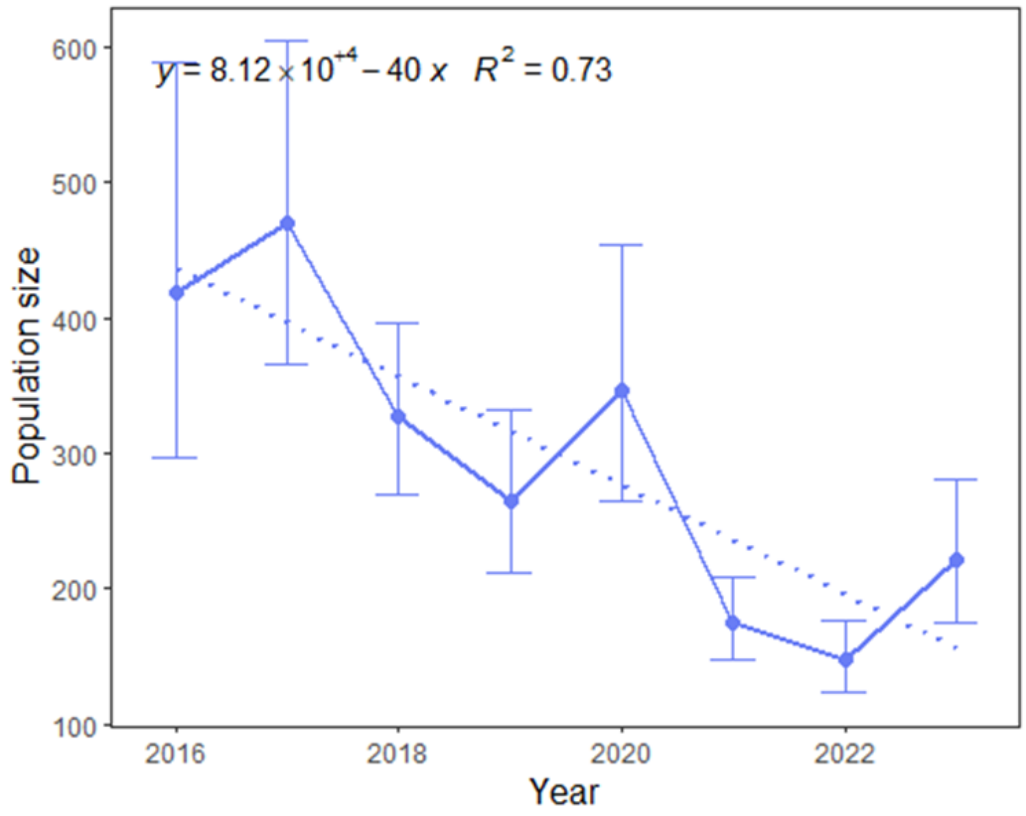

Fig. 29:
Estimated population sizes for Seeschlacht across the study years with a fitted regression line. Population estimates were obtained from the averaged models. Note: Error bars indicate the upper and lower limits of the 95% confidence interval estimated by OpenCR. Adult and juvenile capture events were used for the models (N = 5715).

Groundwater Levels and Population Size

To investigate whether groundwater levels were associated with annual population size, estimated population sizes derived from the JSSAN models were compared with groundwater levels from the previous year. Groundwater data from sensor K2 were used for Königshaufen, while sensor S2 was used for Seeschlacht. Only these monitoring stations were included because they provided complete datasets across the study period. For each study year, the peak monthly mean groundwater level of of the previous year was used for the analyses (Figs. 30-33). Scatterplots and temporal comparisons indicated some similarity in the interannual patterns between groundwater levels and estimated population sizes, particularly in Königshaufen. However, Spearman's rank correlation showed no significant relationship between groundwater levels and estimated population size in Königshaufen ($\rho = 0.26$, $p = 0.536$, $N = 8$) or Seeschlacht ($\rho = 0.17$, $p = 0.703$, $N = 8$). In Königshaufen, population size and groundwater levels showed partially similar temporal trends,

although several years deviated from this pattern (Fig. 32). In Seeschlacht, no clear temporal relationship between groundwater levels and estimated population size was apparent (Fig. 33)

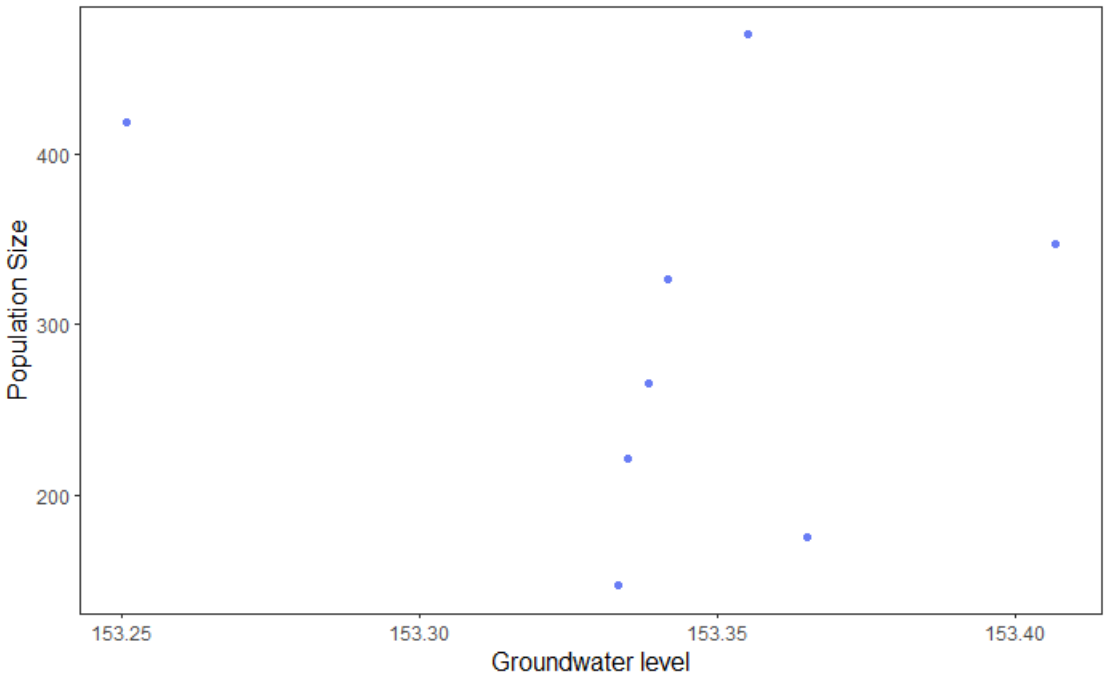

Fig. 30:
Scatterplot for the mean water level per year and the population size for Seeschlacht.
Note: N=8 years, The groundwater level is the peak of the mean monthly groundwater measurements in Sensor S2

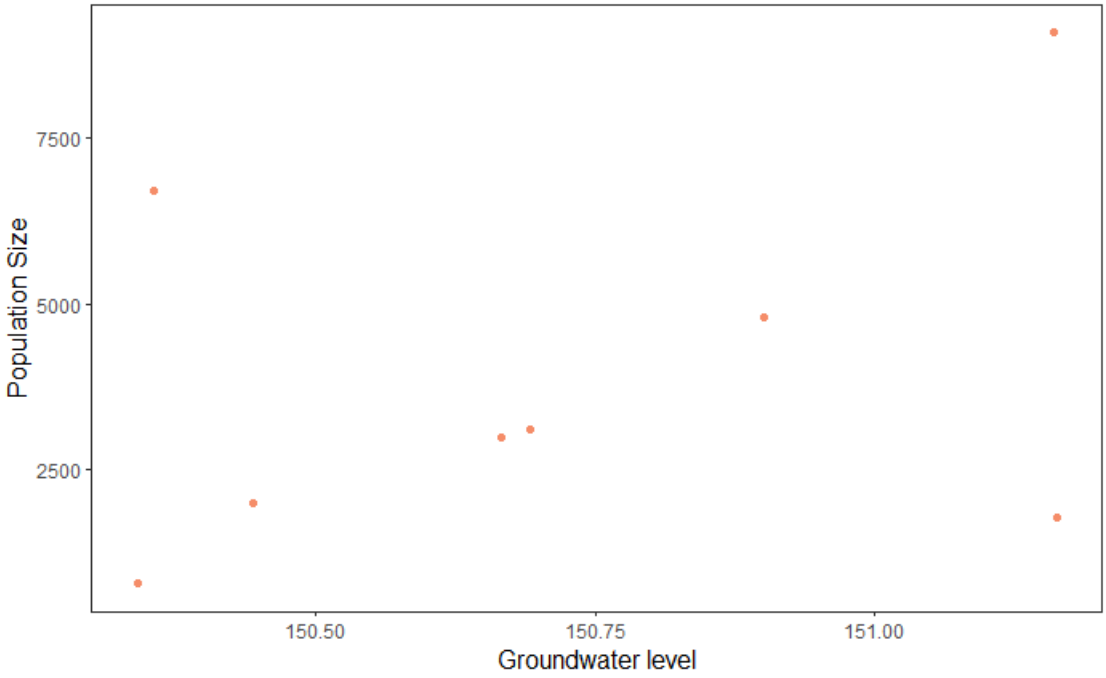

Fig. 31:
Scatterplot for the mean water level per year and the relative amount of Juvenile Captures for Königshaufen.
Note: N=8 years, The groundwater level is the peak of the mean monthly groundwater measurements in Sensor K2

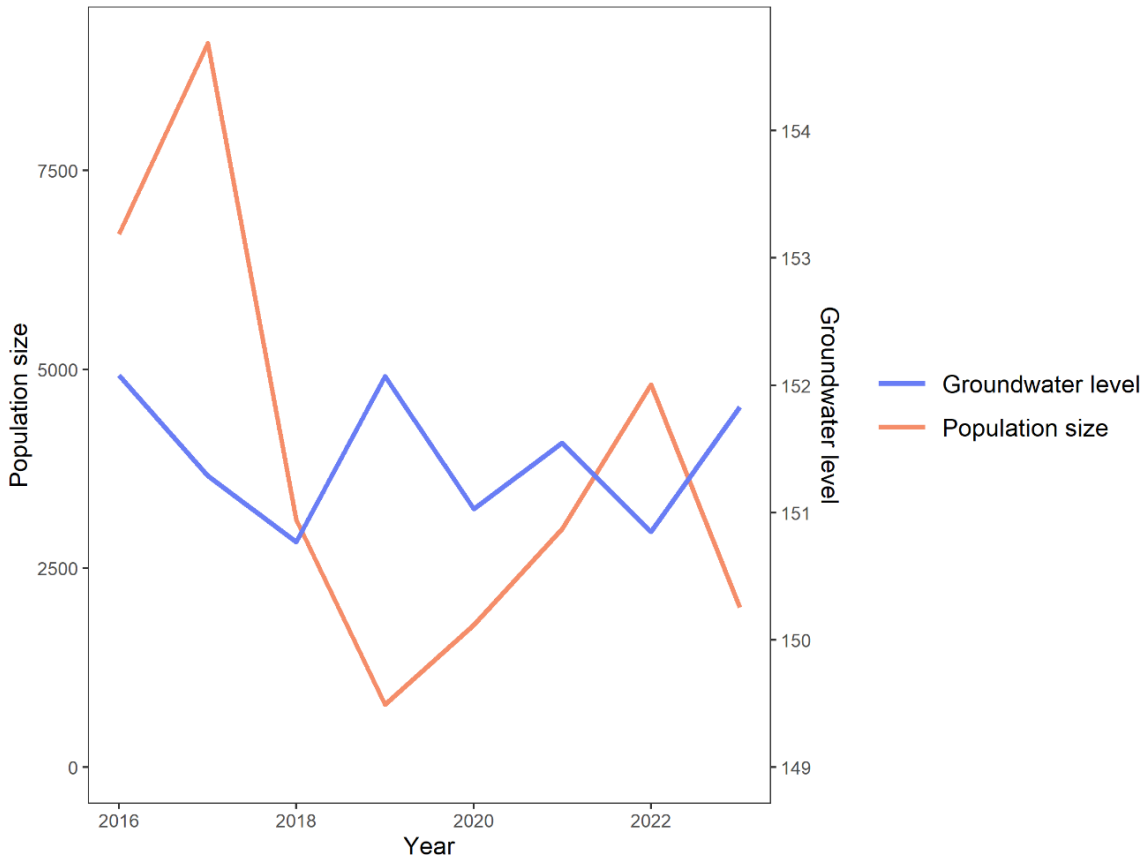

Fig. 32:
Line plot for the Ground Water Levels and estimated Population size in Königshaufen over the study years
Note: The groundwater level is the peak of the mean monthly groundwater measurements in Sensor K2, N=8 years

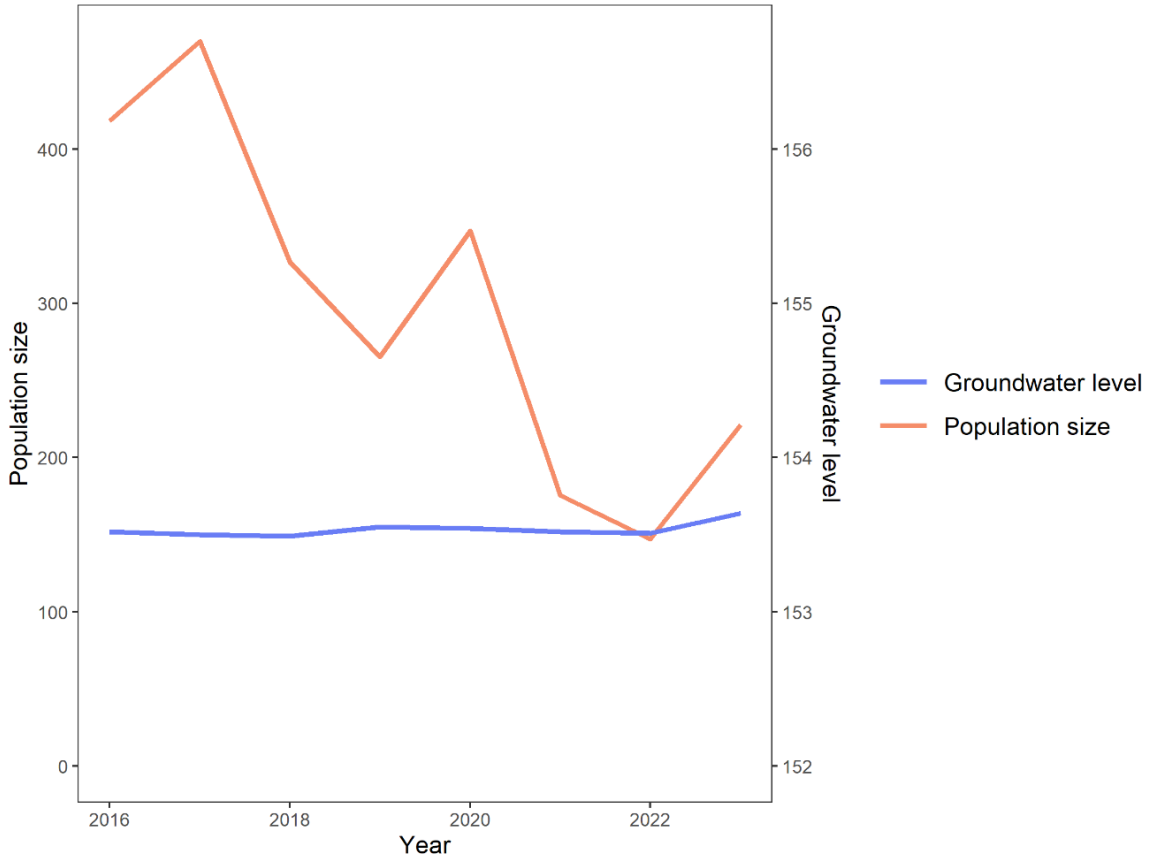

Fig. 33: Line plot for the Ground Water Levels and estimated population size in Seeschlacht over the study years. Note: The groundwater level is the peak of the mean monthly groundwater measurements in Sensor S2, N=8 years

Scaled Mass Index (SMI)

The scaled mass index (SMI) was calculated as a measure of individual fitness following the method described by Peig and Green (2009), using the same approach as Philippi (2013) and Landler (2023). The analysis was based on 4519 observations. Log-transformed body mass and snout–vent length (SVL) were used to estimate the scaling exponent (b) (see Fig. 34).

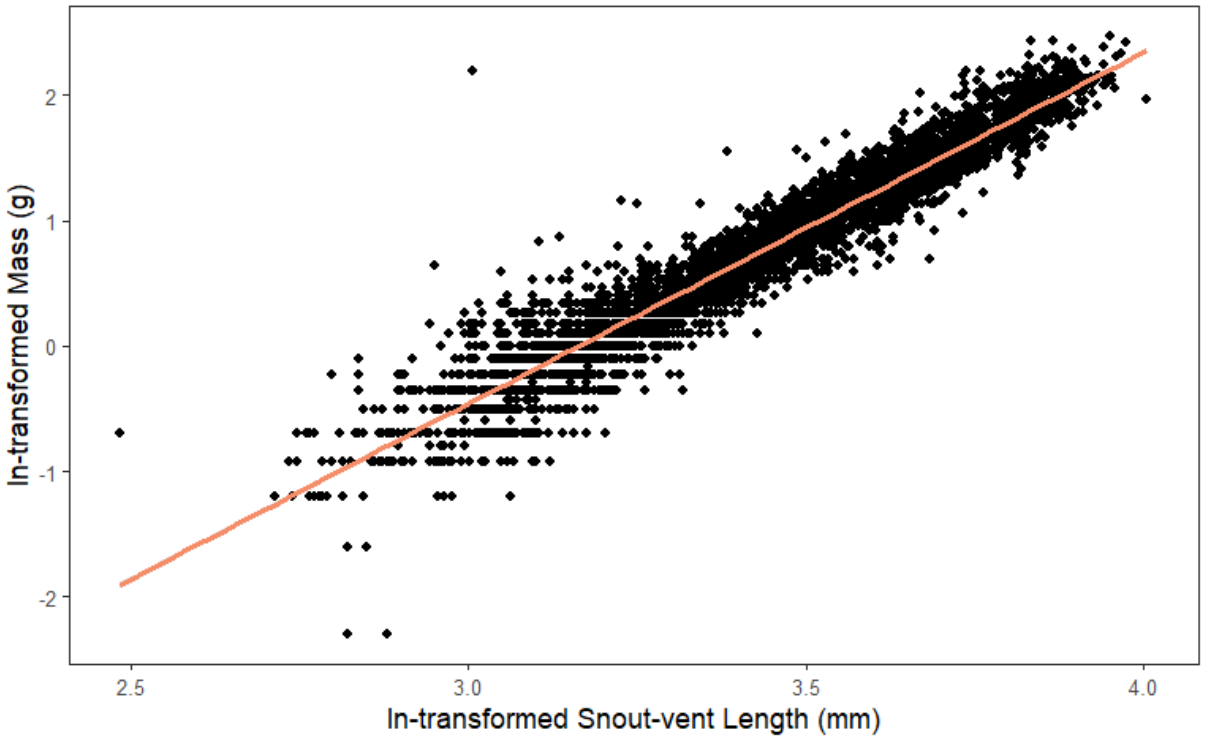

Fig. 34: Scatterplot with regression line for the ln-transformed Mass and Snout-vent Length.
Note: The ln transformed data was used to calculate the exponent b for the SMI calculation. R^2=.92
The first capture event for each individual was used to create this figure (N=4519)

The exponent was calculated using a standardized major axis (SMA) regression from the *smatr* package in R (Warton et al., 2012).

The estimated scaling exponent was b = 2.92 (95% CI [2.90, 2.94]). The mean SVL was M = 31.39 mm, and a reference length of L_0 = 30.00 mm was selected to provide a standardized basis for comparison (see Fig. 35).

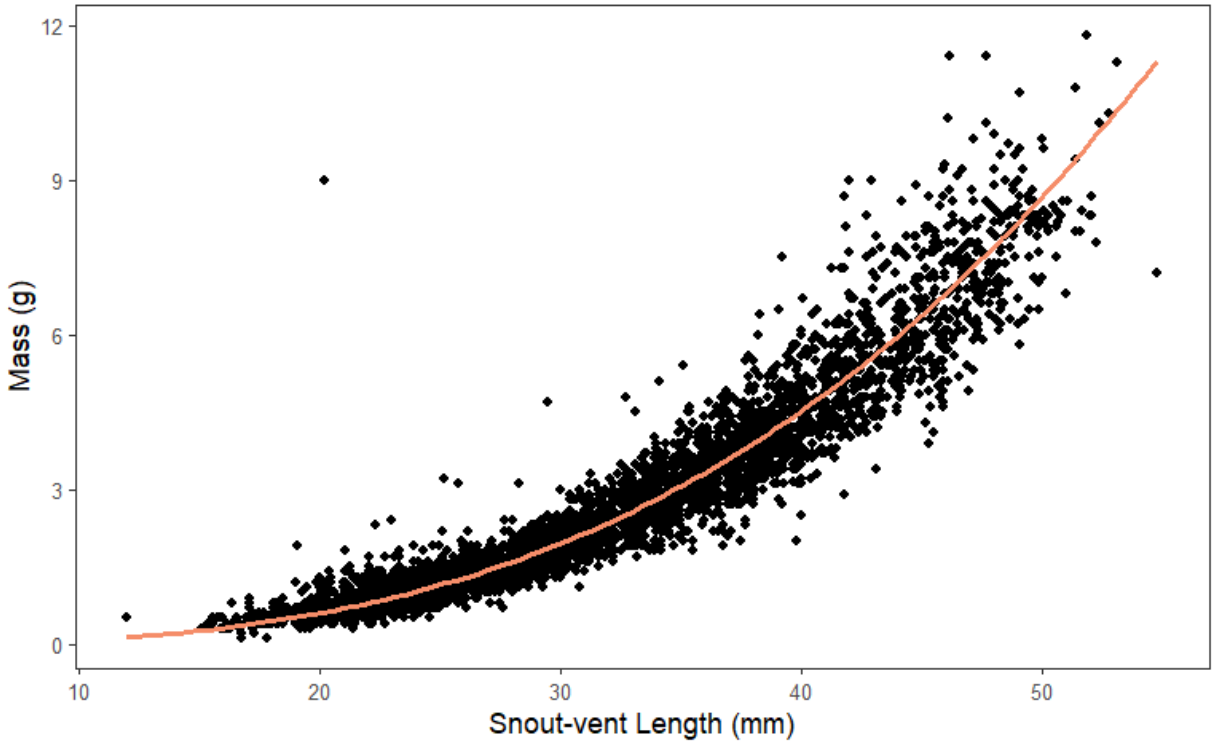

Fig. 35:
Scatterplot with the estimated reference line for the SMI.
Note: The orange line represents the reference for the SMI estimation and it is given by the formula: $M_0*(SVL/SVL_0)^b$ where M_0 is the predicted mass given the reference SVL from the model used for estimating b. The first capture event for each individual was used to create this figure (N=4519).

The formula used to calculate the SMI for each individual is given in Equation 1.

$$SMI = M_i * \left(\frac{L_0}{L_i}\right)^b = M_i * \left(\frac{30}{L_i}\right)^{2.919749}$$

Equation 1: calculation of the SMI with the calculated and chosen parameters.
M_i denotes the mass of the individual, L_i the Snout-Vent Length of each individual, L_0 is the reference length and b is the exponent used in the power function $M=\alpha*L^b$

Size, Mass and SMI between Sites

Annual mean values of snout–vent length (SVL), body mass, and scaled mass index (SMI) varied across study sites and years (Figs. 36-38). While repeated captures of the same individuals were retained in these visualizations, repeated measurements were statistically accounted for in the

mixed-effects models by including individual identity as a random effect. Error bars in the figures represent 95% confidence intervals, highlighting the differences in distribution and temporal variation between Seeschlacht and Königshaufen.

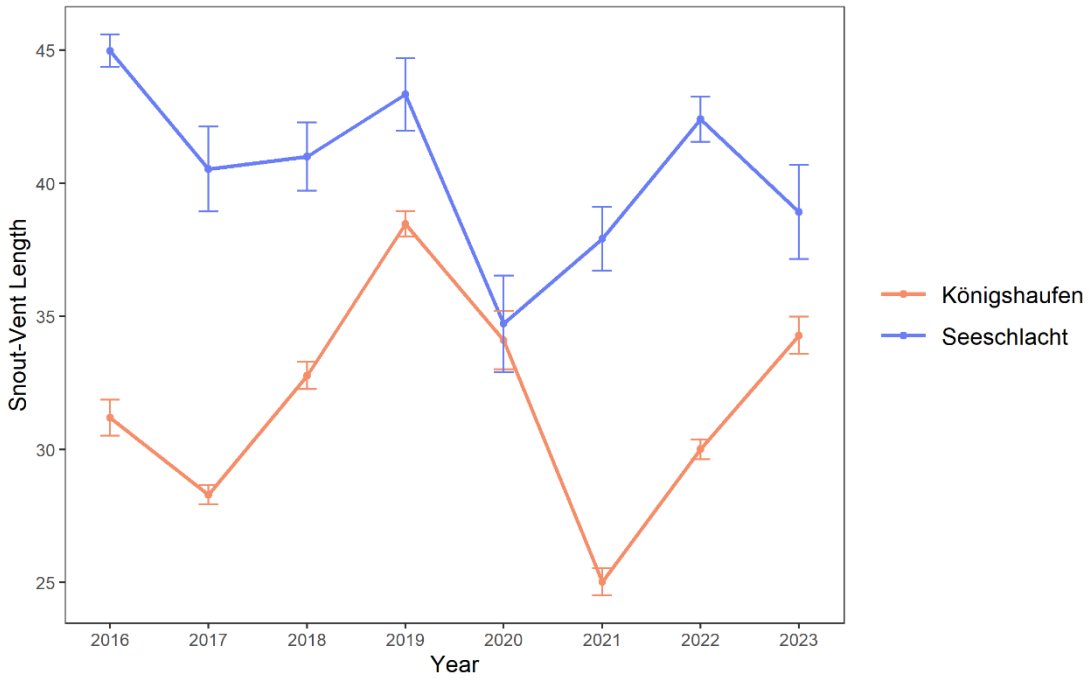

Fig. 36:
Annual mean snout–vent length (SVL) of Bombina bombina in Königshaufen and Seeschlacht between 2016 and 2023. Error bars indicate 95% confidence intervals. Snout-Vent Length was measured in mm (N=5715).

Mean snout–vent length (SVL) was higher in Seeschlacht than in Königshaufen across all study years (Fig. 36). While both populations showed interannual variation, the difference between sites remained relatively stable over time, with individuals from Seeschlacht reaching substantially larger body sizes. Confidence intervals overlapped moderately in some years, yet a clear separation between the two populations remained evident. A similar pattern was observed for body mass, with individuals from Seeschlacht showing higher mean mass throughout the study period, while those from Königshaufen remained lighter (Fig. 37). Temporal fluctuations were evident in both populations, but these did not alter the overall trend of higher body mass in the more stable habitat.

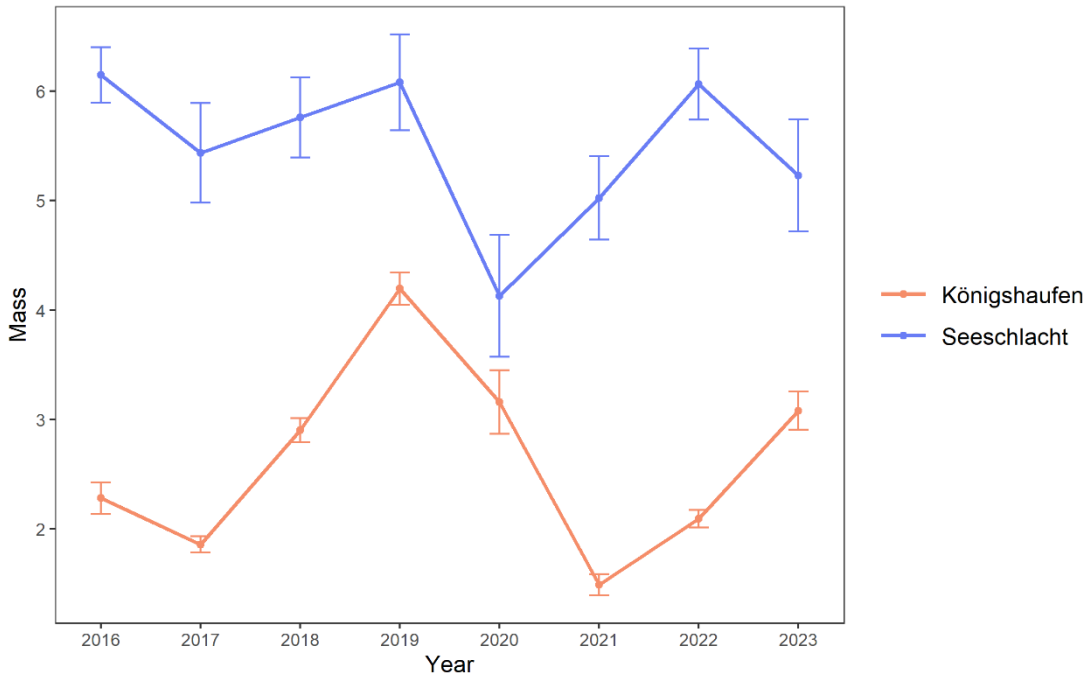

Fig. 37:
Annual mean body mass of Bombina bombina in Königshaufen and Seeschlacht between 2016 and 2023. Error bars indicate 95% confidence intervals (N=5715).

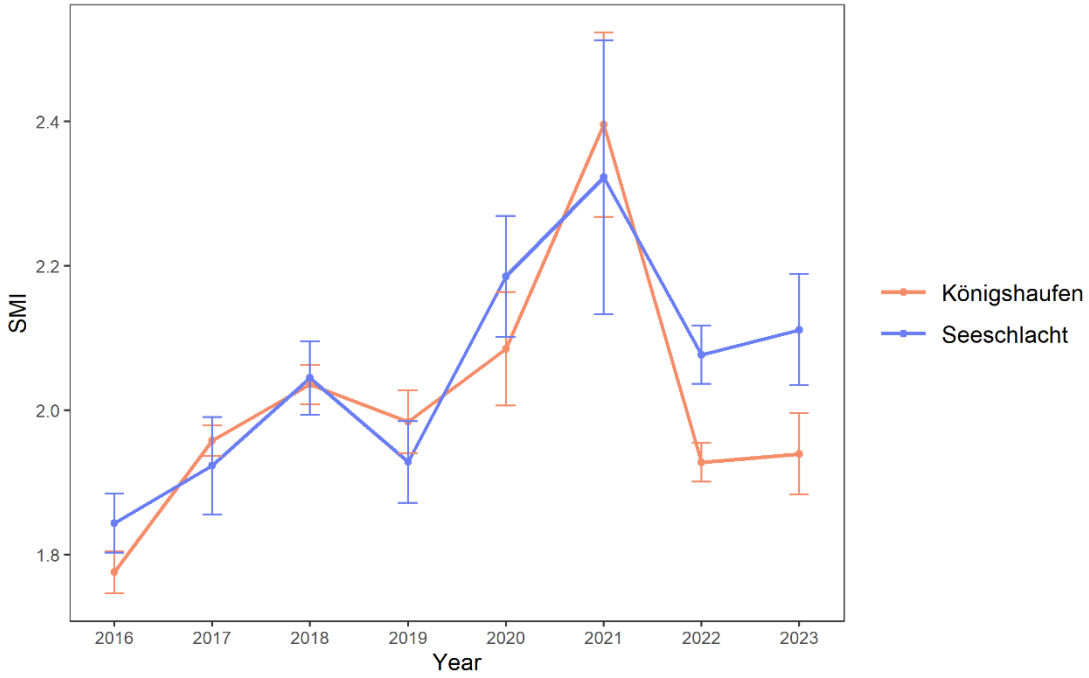

Fig. 38:
Annual mean scaled mass index (SMI) of Bombina bombina in Königshaufen and Seeschlacht between 2016 and 2023. Error bars indicate 95% confidence intervals (N=5715).

Body condition, calculated via the scaled mass index (SMI), varied much less between the populations (Fig. 38). Mean SMI values fluctuated over the years, but a clear separation between

the two sites never emerged. Because the confidence intervals largely overlap, body condition remains comparable across habitats, even though absolute size and mass differ. Animals in Seeschlacht scored slightly higher in certain years, yet this trend lacked consistency over the study period.

Factors influencing Condition (SMI)

A robust linear mixed-effects model evaluated the predictors of body condition, using the scaled mass index (SMI) as the response variable. The analysis accounted for repeated measurements by treating individual identity as a random effect. Fixed effects included study site, year, day of year (DOY), sex, groundwater level, temperature, and precipitation (Table 15; Figs. 39–41). The model revealed a distinct spatial effect: individuals from Seeschlacht maintained higher SMI values than their counterparts in Königshaufen (β = 0.26) (Fig. 39), although their distributions overlapped considerably. Despite noticeable interannual variation, body condition also improved over the study period (β = 0.12) (Fig. 40). Males generally scored higher than females (β = 0.11) (Fig. 41) with a substantial overlap remaining between the sexes. Among the environmental predictors, elevated temperatures correlated with higher SMI scores (beta = 0.16), whereas groundwater levels (centered within sites) showed a significant negative effect (beta = -0.08). Days of the year and precipitation showed no significant effects on SMI.

Table 1
Results of the linear mixed model for the SMI as the outcome Variable.
*Note: the random intercept per individual did not vary for the robust model for the SMI (SD=0.00). The * denotes terms significant at the 0.05 level.*

				95% Confidence Interval		
	Estimate	SE	t	Lower limit	Upper limit	Std Estimate
(Intercept)	-37.37	5.69	-6.56	-48.53	-26.21	
Area (Seeschlacht)	0.09	0.01	7.13	0.07	0.12	0.26*
Year	0.02	0.00	6.83	0.01	0.02	0.12*
Day of year	0.00	0.00	1.84	-0.00	0.00	0.06
Sex (Male)	0.04	0.01	3.21	0.02	0.06	0.11*
Water Level (centered per area)	-0.07	0.02	-3.96	-0.11	-0.04	-0.08*
Temperature	0.01	0.00	4.95	0.01	0.02	0.16*
Precipitation	0.00	0.00	-0.23	-0.00	0.00	0.00

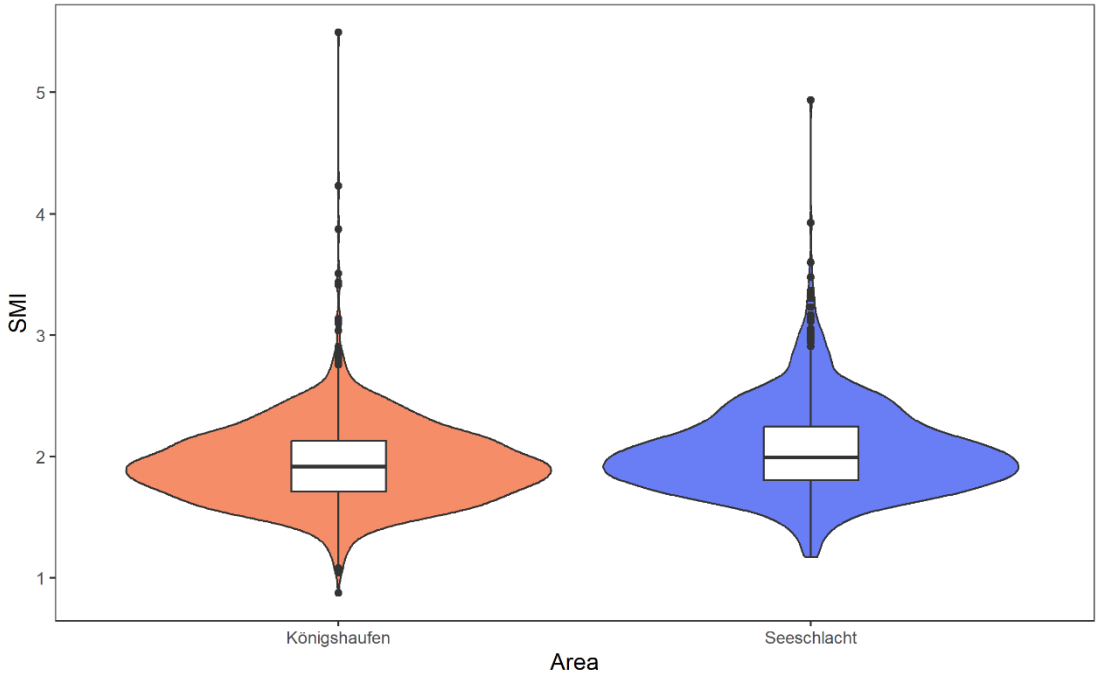

Fig. 39:
Violin Plots for the SMI between Seeschlacht and Königshaufen.
Note: Only adult captures were used for this analysis (N=2583).

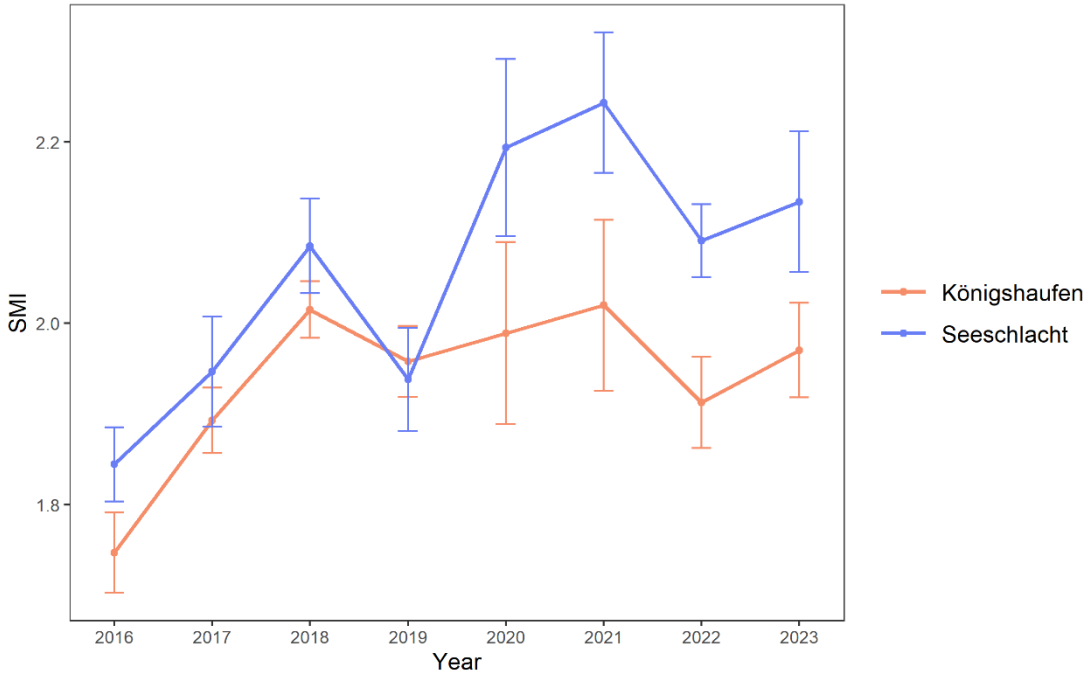

Fig. 40: Line plots for the SMI between Seeschlacht and Königshaufen over the study years. Note: There is a rising trend visible in the data. Note: only adult captures were used for this analysis (N=2583).

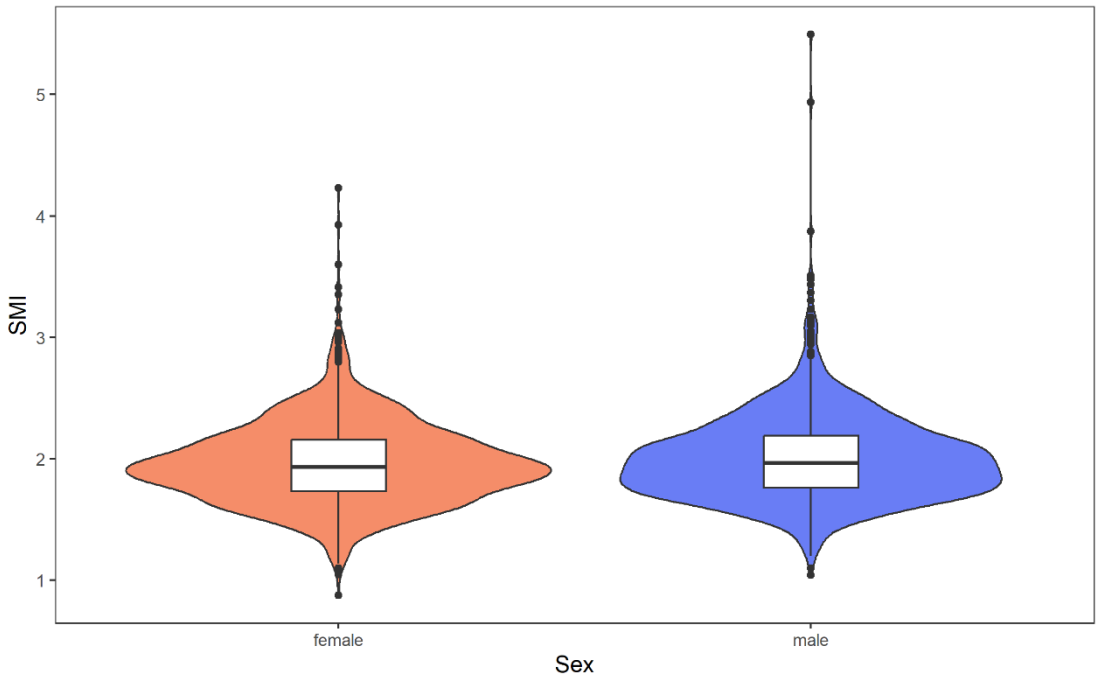

Fig. 41:
Violin Plots for the SMI between Males and Females.
Note: Only adult captures were used for this analysis (N=2583).

Factors influencing SVL

A comparison showed that a null model with varying intercepts for individuals provided a significantly better fit to the SVL data than a model without varying intercepts ($\chi^2(1) = 903.02$, $p < .001$). Due to outliers and deviations from normality of the residuals, a robust model was fitted using the *rlmer* function from the *robustlmm* package (Koller, 2016) (Table 16, Figs. 42-44). The analysis revealed a significant difference between study sites ($\beta = 1.29$), with individuals from Seeschlacht averaging 6.33 mm longer in SVL than those from Königshaufen.

SVL decreased slightly over the study period ($\beta = -0.04$) and was lower in males than in females ($\beta = -0.16$). Higher average temperatures during the month of capture were associated with lower SVL values ($\beta = -0.06$). Groundwater level relative to the site-specific mean was positively linked to SVL ($\beta = 0.06$), indicating that higher water levels matched larger body size. Days of the year and precipitation did not have a significant effect on SVL.

Table 2
Results of the linear mixed model for the SVL as the outcome Variable
*Note: the random intercept per individual varied for the robust model for the SVL (SD=3.00). The * denotes terms significant at the 0.05 level.*

	Estimate	SE	t	95% Confidence Interval		Std Estimate
				Lower limit	Upper limit	
(Intercept)	221.95	67.45	3.29	89.74	354.15	
Area (Seeschlacht)	6.32	0.19	33.57	5.95	6.69	1.29*
Year	-0.09	0.03	-2.71	-0.16	-0.02	-0.04*
Day of year	0.00	0.00	0.97	-0.00	0.01	0.02
Sex (Male)	-0.80	0.17	-4.65	-1.13	-0.46	-0.16*
Water Level (centered per area)	0.72	0.20	3.69	0.34	1.10	0.06*
Temperature	-0.06	0.02	-2.48	-0.10	-0.01	-0.06*
Precipitation	0.00	0.00	1.25	0.00	0.01	0.02

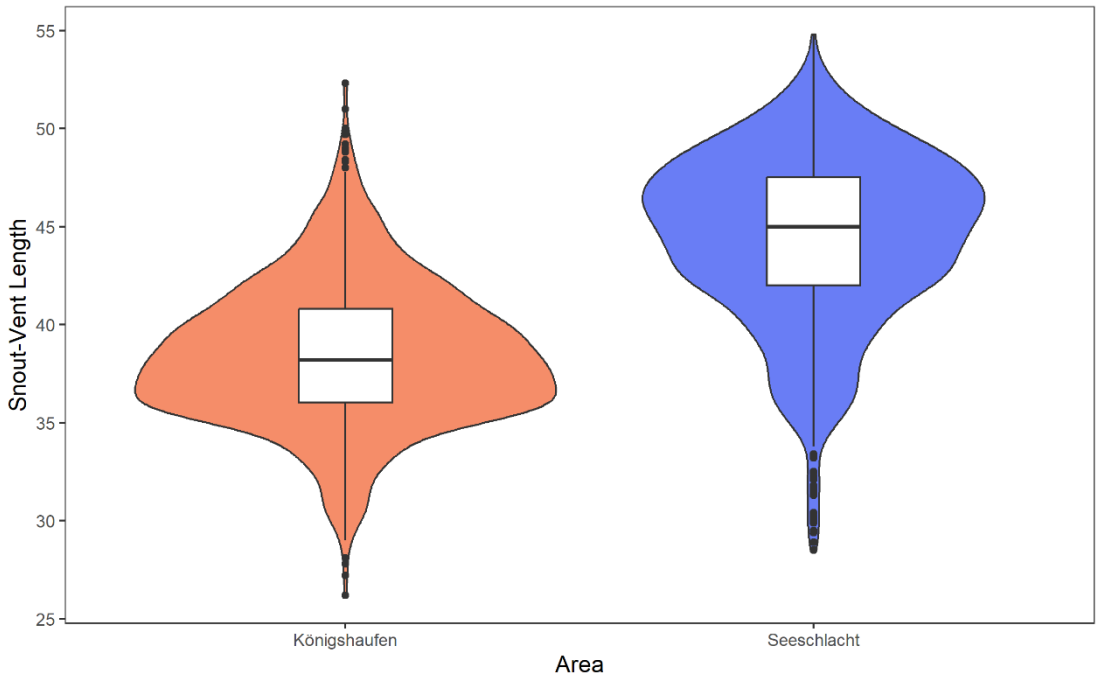

Fig. 42:
Violin Plots for the SVL between Seeschlacht and Königshaufen
Note: Snout-Vent Length was measured in mm. Only adult captures were used for this analysis (N=2583).

The spatial comparison highlights larger body sizes in the Seeschlacht population compared to the Königshaufen area (Figure 42). Despite a substantial overlap between the two distributions, the median SVL shifted notably upward in Seeschlacht

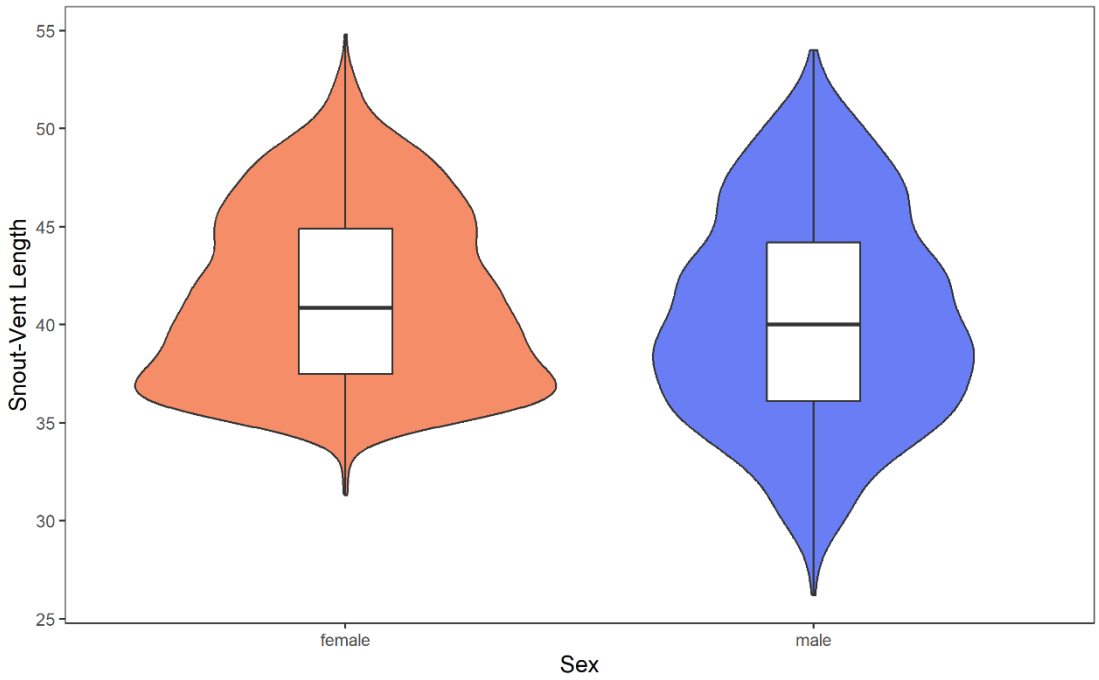

Fig. 43:
Violin Plots for the SVL between male and female toads
Note: Snout-Vent Length was measured in mm. Only adult captures were used for this analysis (N=2583).

Regarding sex-specific differences, females generally reached larger body sizes than males (Figure 43). Although the data distributions overlapped considerably, the median SVL shifted visibly downward in males.

Over the study period, SVL fluctuated moderately between years in both populations (Figure 44). Despite this interannual variation, individuals from Seeschlacht remained consistently larger than those from the Königshaufen area.

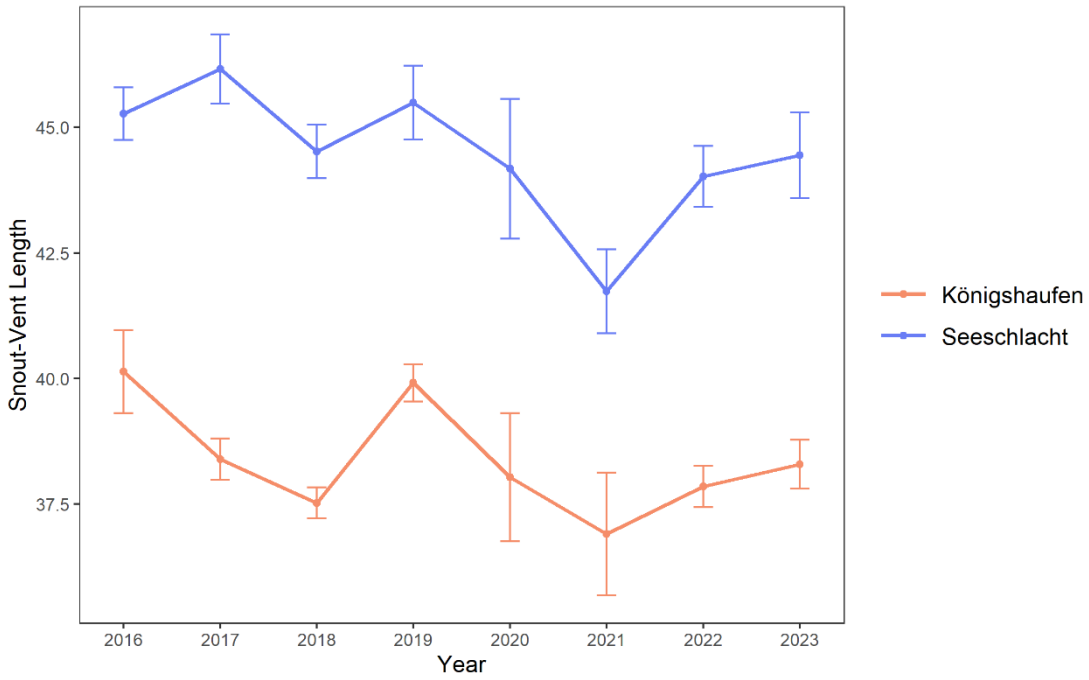

Fig. 44:
Line Plot for the SVL between sites across years
Note: Snout-Vent Length was measured in mm. Only adult captures were used for this analysis (N=2583).

Factors influencing Mass

A comparison showed that a null model with varying intercepts for individuals provided a significantly better fit to the body mass data than a model without varying intercepts ($\chi^2(1) = 1167.06$, $p < .001$). To address outliers and deviations from the normality of the residuals, a robust model was fitted using the *rlmer* function from the *robustlmm* package (Koller, 2016; Table 17; Figs. 45-47). The analysis revealed a clear difference between study sites ($\beta = 1.34$), with individuals from Seeschlacht being on average 2.56 g heavier than those from Königshaufen. Furthermore, body mass increased slightly over the course of the year ($\beta = 0.07$) while males remained lighter than females ($\beta = -0.07$). Environmental factors - including temperature, precipitation, and site-centered groundwater levels - had no significant influence on mass, nor did the factor year.

Table 3
Results of the linear mixed model for Mass as the outcome Variable.
*Note: the random intercept per individual varied for the robust model for the Mass (SD=1.22). The * denotes terms significant at the 0.05 level.*

				95% Confidence Interval		
	Estimate	SE	t	Lower limit	Upper limit	Std Estimate
(Intercept)	-39.57	23.62	-1.68	-85.85	6.72	
Area (Seeschlacht)	2.56	0.07	37.48	2.43	2.69	1.34*
Year	0.02	0.01	1.83	-0.00	0.04	0.03
Day of year	0.00	0.00	3.19	0.00	0.01	0.07*
Sex (Male)	-0.14	0.06	-2.19	-0.26	-0.01	-0.07*
Water Level (centered per area)	0.13	0.07	1.95	-0.00	0.27	0.03
Temperature	0.00	0.01	-0.23	-0.02	0.01	0.00
Precipitation	0.00	0.00	0.44	-0.00	0.00	0.01

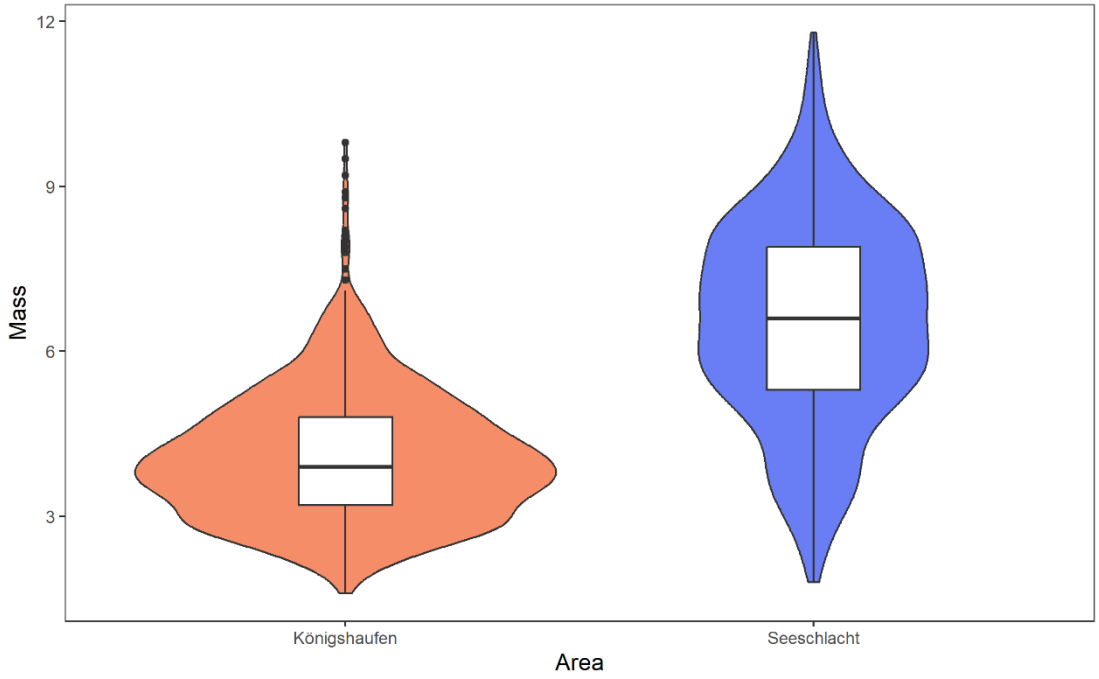

Fig. 45:
Violin Plots for the Mass between Seeschlacht and Königshaufen
Note: Mass was measured in g. Only adult captures were used for this analysis (N=2583).

Body mass differed markedly between the study sites. Despite overlapping distributions, the mean values were substantially higher in toads from Seeschlacht than in those from Königshaufen (Figure 45).

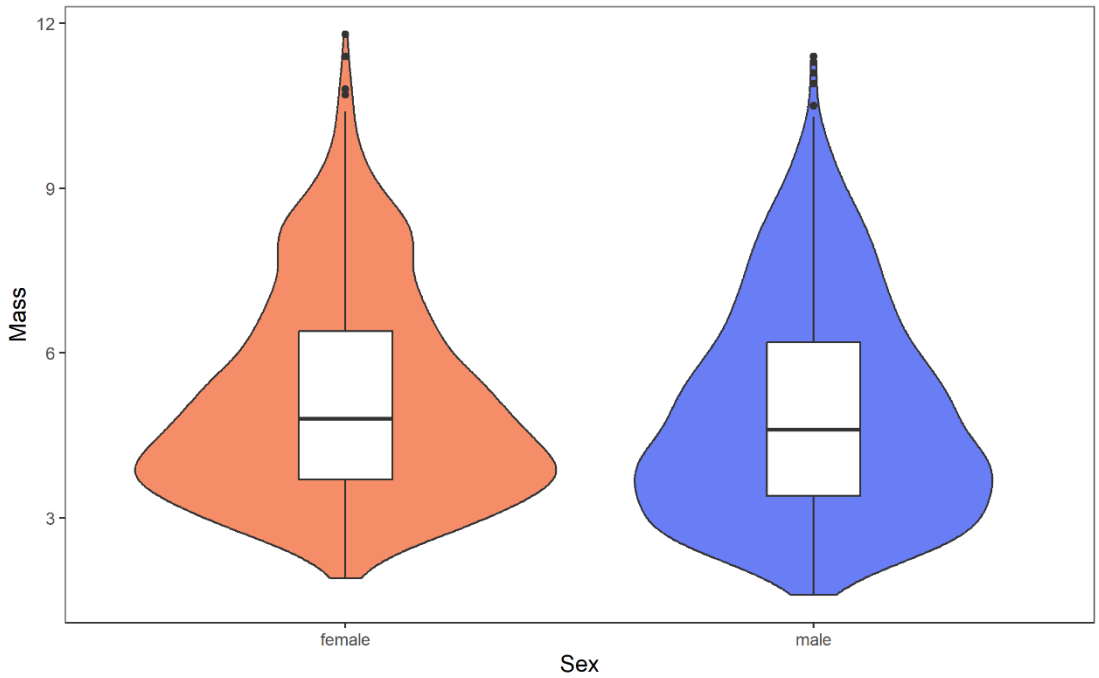

Fig. 46:
Violin Plots for the Mass between male and female toads.
Note: Only adult captures were used for this analysis (N=2583).

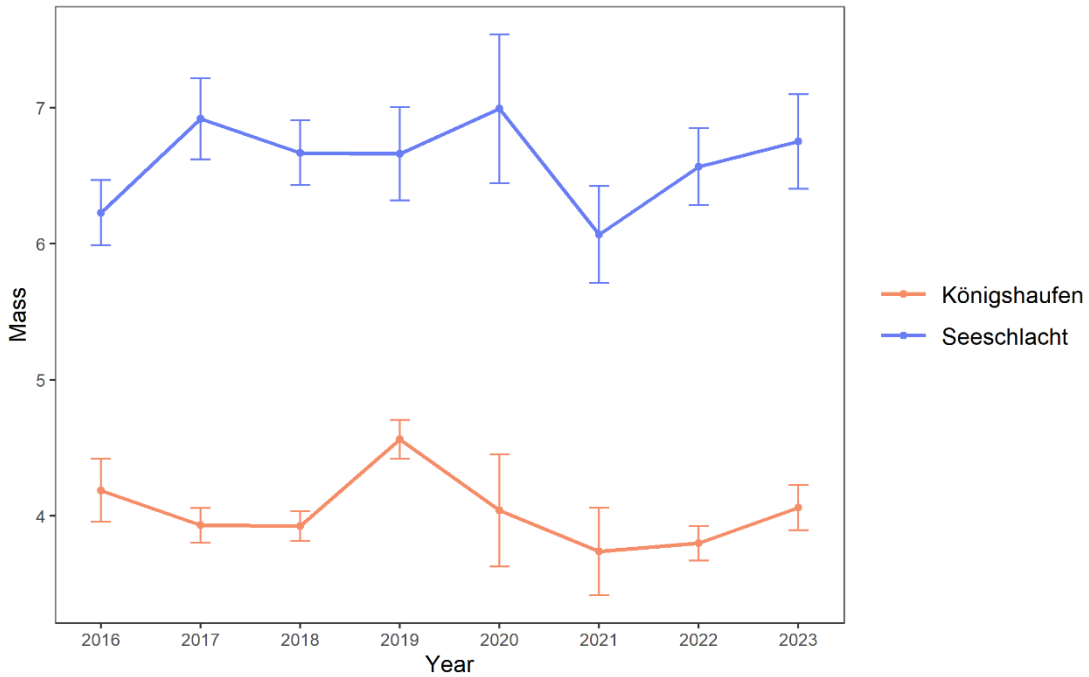

Fig. 47:
Line Plot for the Mass between sites across years
Note: Mass was measured in g. Only adult captures were used for this analysis (N=2583).

Body mass was highly comparable between the sexes (Figure 46). While females maintained a slightly higher median mass than males, their overall data distributions overlapped almost

entirely. Interannual variations in body mass remained moderate across both study sites (Figure 47). Although values fluctuated from year to year, individuals from Seeschlacht stayed consistently heavier than those from the Königshaufen area.

Discussion

The present study identified clear contrasts between the two *Bombina bombina* populations in demographic parameters, body size and body condition, reflecting the differing ecological characteristics of the two study sites. These patterns are also evident in the JSSAfCL models, which show higher apparent survival in Seeschlacht and higher per capita recruitment in Königshaufen, consistent with previous findings by Huemer (2023). The higher apparent survival in Seeschlacht suggests more favourable long-term conditions in this habitat. In Königshaufen, the trend was reversed. Apparent survival was considerably lower than in Seeschlacht and may be related to increased environmental variability, higher dispersal rates, or increased predation pressure, as also discussed by Huemer (2023). At the same time, per capita recruitment was considerably higher in Königshaufen than in Seeschlacht. This dynamic aligns with the elevated reproductive output typical of ephemeral breeding sites, where temporary water bodies offer optimal conditions for larval development despite their limited duration (Huemer, 2023; Schedl et al., 2009). The divergence between the two study sites illustrates a clear survival–recruitment trade-off, reflecting a distinct shift along the slow–fast life-history continuum driven by habitat stability. By quantitatively linking these demographic shifts to variations in body size, mass, and condition, this study provides a deeper insight into how *Bombina bombina* adapts its life-history strategies across the two contrasting habitats of the Lobau.

As mentioned by Philippi and Gollmann (2014), the degree of connectivity between the two study sites remains uncertain. Although no individuals were recaptured between Seeschlacht and Königshaufen during the study period, movement between sites cannot be entirely excluded, particularly for juvenile individuals. The two populations may therefore represent semi-independent subpopulations within a larger metapopulation system, potentially linked through dispersal processes. In this context, Königshaufen could function as a highly productive source habitat, whereas Seeschlacht may represent a more stable but less productive habitat (Czurda et al., 2023).

Capture Probability

Capture probability varied considerably between study sites, years, sexes, and demographic groups. Across both model frameworks (JSSAfCL and JSSAN), probabilities were consistently higher in Seeschlacht than in Königshaufen. Such variation in detectability is a common feature of capture–recapture studies. If not adequately accounted for, it biases population estimates (Schmidt, 2004; Kellner and Swihart, 2014). The higher detectability in Seeschlacht reflects habitat structure and hydrological stability rather than differences in activity alone. Stable environmental conditions lead to predictable spatial use of water bodies, which increases recapture success. In contrast, the dynamic hydrology in Königshaufen forces individuals to disperse widely. Strong groundwater fluctuations directly alter accessibility to breeding ponds. During high-water periods, deeper sections become difficult to sample. Conversely, dry phases force toads to retreat into moist terrestrial microhabitats, reducing capture success. Increased mobility and flight distances in open water may further lower detectability, as previously noted for *Bombina bombina* (Gollmann et al., 2013). According to the JSSAN models, juveniles had the highest capture probabilities, while adult males showed the lowest. Behavioural differences likely drive this pattern. Juveniles and inactive individuals frequently stay in shallow shoreline areas, making them easier to spot and catch**.** Adult males are acoustically conspicuous during calling activity, thereby drawing predator attention. They compensate by maintaining high vigilance and rapid escape responses. These behaviours became obvious during fieldwork. Females and juveniles typically stayed close to the water surface and hid in nearby vegetation over short distances. Adult males often dived immediately. They remained submerged for extended periods and were difficult to relocate afterwards. Furthermore, males showed intense escape responses during handling and morphometric measurements (Philippi, 2013). Habitat structure also influenced detectability. In Seeschlacht, aquatic and shoreline vegetation became increasingly high and dense over the course of the season, making visual detection of individuals much more difficult. At the same time, this dense vegetation likely reduced predation pressure by providing additional cover and refuge structures for the toads. Due to the large size and limited accessibility of the study area, many habitat areas could not be surveyed. Temporal variation in capture probability across years was likely influenced by a combination of environmental and methodological factors. Sampling effort varied considerably among years, particularly during the COVID-19 pandemic, when fieldwork was delayed and the number of field trips was reduced. Lower sampling intensity in 2020 and partially in 2021 likely

contributed to reduced capture probabilities during these years, whereas increased sampling effort in later years led to higher estimates. Factors not fully accounted for in the models, including individual heterogeneity and temporary emigration, may also affect capture probability. Individuals temporarily absent from the study area effectively have a capture probability of zero, which can bias estimates of survival and population size (Fujiwara and Caswell, 2002). Such processes are likely particularly relevant in dynamic habitats such as Königshaufen, where movement between ponds and temporary absence from breeding sites are expected**.** Temporary emigration can also result from reproductive skipping, which has been described in amphibians inhabiting variable environments (Muths et al., 2006). The extent of this bias remains unknown but should be considered when interpreting demographic parameters.

Life history variation

Apparent survival

Apparent survival differed markedly between the two study sites and was consistently higher in Seeschlacht than in Königshaufen. These pronounced differences also support the importance of habitat stability for long-term population survival. The relatively high survival rates observed in Seeschlacht indicate that stable hydrological conditions reduce mortality risks and allow individuals to persist over multiple years. In contrast, the considerably lower apparent survival in Königshaufen reflects the more dynamic and unpredictable nature of this habitat. When interpreting these estimates, it must be considered that apparent survival combines true survival with permanent emigration, meaning mortality cannot be distinguished from the permanent loss of individuals from the study area (Ergon and Gardner, 2014; Gilroy et al., 2012).

The lower apparent survival estimates in Königshaufen may therefore partly reflect increased movement and dispersal behaviour in response to fluctuating environmental conditions. Strong and stochastic changes in water levels can force individuals to leave temporarily unsuitable areas or shift their spatial distribution. This displacement directly reduces recapture probabilities and lowers apparent survival estimates. Similar patterns have been described in other *Bombina* species inhabiting unpredictable environments. Cayuela et al. (2016b) reported lower apparent survival in populations of *Bombina variegata* occupying highly dynamic breeding habitats. They

suggested that increased dispersal and its associated energetic costs lower overall survival. Additional studies demonstrated higher intra- and interannual dispersal rates under unpredictable environmental conditions (Cayuela et al., 2016d). Such trade-offs between survival and dispersal align with life-history theory and likely play an important role in Königshaufen. Higher mortality rates in Königshaufen may additionally contribute to the observed differences. The concentration of amphibians and other prey species within a limited number of breeding sites likely attracts a higher density of predators than in Seeschlacht. Predators such as grey herons (*Ardea cinerea*) and grass snakes (*Natrix natrix*) are regularly observed in the area. Furthermore, the horse leech (*Haemopis sanguisuga*) occurs in large numbers at the Königshaufen site. It is a predator of spawn and tadpoles that is also well adapted to the fluctuating conditions. Although *Bombina bombina* possesses chemical skin toxins, adult individuals are still susceptible to predation (Gollmann et al., 2012). Increased movement activity further elevates mortality risk. The population structure and recapture frequencies also reflect the differences in apparent survival. Individuals in Seeschlacht were recaptured more frequently and likely reached higher ages, indicating greater longevity under stable environmental conditions. Populations inhabiting dynamic floodplain habitats such as Königshaufen display an opposite trend; they are characterized by shorter lifespans and stronger population turnover.

Per Capita Recruitment

Per capita recruitment was substantially higher in Königshaufen than in Seeschlacht, indicating clear differences in reproductive success and habitat suitability between the two study sites. The high recruitment rates observed in Königshaufen demonstrate that the ponds are highly suitable breeding habitats for *Bombina bombina*. The larger numbers of juveniles and metamorphs recorded throughout the study period directly reflect this. Several habitat characteristics likely contribute to the higher reproductive success in Königshaufen. The ponds are largely open, sun-exposed, and characterized by fluctuating hydroperiods. These conditions are generally considered favourable for the reproduction and tadpole development of *Bombina bombina* (Schedl, 2005; Gollmann et al., 2012). Temporary water bodies often support lower abundances of aquatic predators and therefore increase larval survival (Skelly, 1997). In addition, the shallow, warm, and oxygen-rich water combined with higher primary productivity accelerate egg and larval development. The lower recruitment observed in Seeschlacht indicates less favourable reproductive conditions. Some

of the water bodies are heavily shaded, resulting in lower water temperatures and reduced solar radiation. Cooler conditions delay egg and larval development, while oxygen-poor and muddy conditions negatively affect egg survival. Submerged aquatic vegetation is also largely absent in many ponds, limiting primary productivity and habitat quality for larval development. Königshaufen offers highly suitable conditions for reproduction, but the habitat is strongly shaped by hydrological instability. Early desiccation of ponds leads to complete reproductive failure in some years if larval development cannot be completed before water levels decline. Nevertheless, the high reproductive success during favourable years appears sufficient to compensate for some years with poor recruitment. By definition, per capita recruitment is a relative measure. It defines the number of new individuals entering a class at time *t*, scaled by the population already present at time $t - 1$ (Efford, 2024). Differences in recruitment rates therefore reflect population structure rather than absolute offspring production. In habitats with lower numbers of individuals in a given class, per capita recruitment can appear elevated even if absolute recruitment is moderate (Huemer 2023). In Königshaufen, the high rates likely reflect both increased reproductive investment and a demographic response to environmental instability. Unpredictable breeding sites often favour high reproductive effort during optimal windows, triggering strong but short-lived recruitment pulses.

Population Size and Temporal Dynamics

Amphibian populations are characterized by pronounced fluctuations in size and demographics when observed over several years. A combination of weather conditions, habitat quality, food availability, and predation risk drives these dynamics. In this study, estimated population sizes differed markedly between the two sites and followed contrasting trajectories. Population size was consistently higher in Königshaufen than in Seeschlacht throughout the study period. This reflects a clear difference in overall abundance between the two habitats. In Königshaufen, population size was characterized by pronounced interannual shifts, with sharp increases and declines between consecutive years. Such variability typifies populations in dynamic environments, where reproductive success and habitat availability vary from year to year. High recruitment rates of young individuals are likely to amplify these fluctuations, as population size strongly depends on reproductive success in the preceding year (Huemer, 2023). In contrast, population size in Seeschlacht followed a more stable temporal trajectory with lower interannual variability, indicating a more buffered population dynamic. A gradual decline over the study period was,

however, observed, suggesting that stable conditions do not necessarily result in increasing population size. These patterns reflect the underlying demographic processes. In Königshaufen, high recruitment combined with lower survival leads to rapid but short-lived increases in population size, followed by declines in less favourable years. In Seeschlacht, higher survival but lower recruitment results in more stable, yet gradually changing population sizes. These results highlight the importance of habitat stability in shaping population size and temporal dynamics. In variable habitats such as Königshaufen, groundwater levels likely affect the availability, size, and hydroperiod of breeding ponds. High water levels during the reproductive season prevent premature desiccation and allow successful larval development. Conversely, low groundwater levels can result in reproductive failure when breeding sites dry out before metamorphosis is completed. The pronounced population decline in Königshaufen observed in 2019 reflects reduced reproductive success during the preceding year. Groundwater levels in 2018 were comparatively low, and temporary desiccation of breeding ponds may have negatively affected larval development and metamorph survival. Huemer (2023) described similar mechanisms for this study system. Since the correlations in this study remained weak and statistically non-significant, these relationships should be interpreted with caution. In Seeschlacht, the gradual decline in population size may also reflect ongoing succession and terrestrialisation. Increasing reed growth, shading, and the progressive overgrowth of formerly open water bodies likely reduce suitability for successful reproduction and larval development. Although individuals often maintain comparatively high SMI values, reproductive success appears to depend primarily on habitat quality rather than energetic condition alone. Suboptimal breeding sites, combined with high predation pressure on tadpoles by dragonfly larvae and diving beetles, likely contribute to the low reproductive output observed in Seeschlacht. Recent hydrological restoration measures in the Obere Lobau might affect future population development in Seeschlacht. Since 2023, additional water from the Neue Donau has been supplied to parts of the floodplain to improve water availability and slow down ongoing terrestrialisation.

Size, Mass and Scaled Mass Index between Sites

Body size and mass differed markedly between the two study sites. Individuals from Seeschlacht reached larger sizes and higher body mass than those from Königshaufen. Although interannual variation was present in both populations, the separation between sites remained relatively constant

over time. This pattern aligns with the demographic differences observed between the populations, particularly the higher survival rates in Seeschlacht and the increased recruitment in Königshaufen. However, differences in mean body size and mass must be interpreted in the context of population structure. The higher mean values observed in Seeschlacht largely reflect the greater proportion of adult individuals in this habitat, whereas the lower values in Königshaufen are primarily driven by the higher proportion of juveniles. Differences in average size and mass do thus not necessarily indicate intrinsic differences in growth performance, but rather differences in age composition between the populations. Nevertheless, the data points to underlying ecological differences between the two habitats. Stable hydrological conditions in Seeschlacht provide a predictable environment with sustained resource availability. This facilitates continuous growth and larger body sizes. In contrast, individuals from Königshaufen tend to remain smaller and lighter, matching the more dynamic and unpredictable nature of this habitat. Periodic desiccation of breeding sites, high population densities during dry phases and restricted foraging opportunities likely limit resource availability and constrain somatic growth. In addition, these conditions appear to promote earlier maturation, as observed during field sampling. This pattern suggests a shift in energy allocation, where individuals invest more heavily in reproduction at the expense of growth. Such a trade-off aligns with life-history theory. In environments with high mortality risk and temporal instability, selection favours earlier reproduction over long-term somatic development (Reznick et al., 1990; Cayuela et al., 2016c). In Seeschlacht, where environmental conditions are more stable but suitable breeding opportunities are limited, individuals may benefit from allocating more energy to growth and maintenance, resulting in larger body size and increased longevity.

Despite these clear differences in absolute size and mass, body condition, as measured by the scaled mass index (SMI), showed no clear separation between the two populations. Although individuals from Seeschlacht tended towards slightly higher SMI values, the distributions largely overlapped. Differences between sites remained small relative to overall variability. Instead, variation in SMI was primarily driven by interannual fluctuations rather than by site-specific effects. These findings suggest that, while environmental conditions strongly influence growth and resulting body size, individuals in both habitats maintain a broadly comparable energetic condition relative to their size. The interpretation of SMI could be further refined by considering seasonal variation within years. During the breeding season, increased reproductive activity often depletes energy reserves, whereas periods following reproduction allow for recovery and body mass accumulation. However,

clear trends might be difficult to detect because *Bombina bombina* is a prolonged breeder. As a result, repeated fluctuations in SMI can occur during reproductive periods without a clear overall pattern emerging. More pronounced changes are therefore likely to occur primarily during the transition from juvenile to adult stages. The tendency towards slightly higher SMI values in Seeschlacht is nevertheless consistent with the ecological differences between the two habitats. In Königshaufen, individuals appear to prioritize early reproduction over long-term energy storage, a pattern documented for amphibians in unpredictable environments (Cayuela et al., 2016c). Therefore, SMI values require cautious interpretation. High body condition does not automatically indicate higher overall fitness; it can also reflect limited opportunities for reproduction. Consequently, similar SMI values between populations do not imply identical ecological conditions, but rather comparable energetic states shaped by different life-history strategies.

Factors Influencing Condition (SMI)

The mixed model indicates that body condition (SMI) is influenced by a combination of spatial, temporal, and environmental factors, although overall effect sizes remained moderate. Individuals from Seeschlacht reached higher SMI values than those from Königshaufen, suggesting slightly better body condition in the more stable habitat.

This pattern aligns with the ecological differences between the sites, where more predictable environmental conditions favour greater investment in somatic maintenance. Furthermore, SMI increased over the study period, indicating a gradual improvement in body condition across years. This trend could reflect broader environmental changes, such as increasing temperatures or improved habitat conditions, although the underlying drivers cannot be clearly disentangled. Males showed slightly higher SMI values than females, which may be related to differences in reproductive investment. Females allocate more energy to egg production, which can temporarily reduce body condition, whereas males invest less in gamete production and therefore maintain higher energy reserves. Temperature had a positive effect on SMI, suggesting that warmer conditions enhance foraging success or metabolic efficiency, thereby improving body condition. This matches with the general importance of temperature for amphibian physiology and activity. The negative effect of groundwater level on SMI should be interpreted with caution, as groundwater levels were centered within each study site to account for multicollinearity with the site variable. As a result, the estimated effect reflects deviations from the site-specific mean rather

than absolute differences between sites. This implies that short-term increases in water levels relative to the local baseline are linked to slightly reduced body condition, whereas overall differences between sites are captured by the site effect itself. Given that Seeschlacht generally features higher groundwater levels than Königshaufen, the positive site effect likely mirrors these broader environmental differences. Consequently, the observed relationship between groundwater level and SMI does not contradict the overall pattern of higher body conditions in Seeschlacht but rather highlights the importance of separating within-site variation from between-site differences in environmental conditions.

Factors Influencing SVL

The results of the SVL model indicate that body size is primarily shaped by spatial and biological factors, with environmental effects playing a secondary role. The strong positive effect of study site confirms that individuals from Seeschlacht reach substantially larger body sizes than those from Königshaufen. This pattern aligns with the ecological differences between the two habitats, supporting the interpretation that more stable environmental conditions allow for prolonged growth and increased longevity. Females had larger SVL values than males, which is consistent with sexual size dimorphism commonly observed in amphibians. Larger female body size is likely associated with reproductive advantages, as it enables higher fecundity and greater egg production. The slight decrease in SVL over the study period may reflect changes in population structure, such as a higher proportion of younger individuals in later years, rather than true reductions in individual growth potential.

Environmental effects on SVL were present but relatively weak. The positive relationship with groundwater level suggests that higher water availability supports increased growth, possibly through improved habitat quality or resource availability. In contrast, the negative effect of temperature might indicate that higher temperatures are associated with increased metabolic costs or environmental stress, potentially limiting somatic growth. Overall, these results suggest that body size is influenced by a combination of habitat conditions and life- history processes, with long-term factors such as growth duration and survival playing a more important role than short-term environmental variation. The opposing directions of effects observed for SVL and SMI further highlight the importance of distinguishing between absolute body size and relative body condition. While factors such as groundwater level were correlated with increased body size (SVL), they were

simultaneously linked to lower SMI values. This pattern likely reflects the fact that SMI represents body mass relative to body size, meaning that increases in body length are not necessarily accompanied by proportional increases in body mass. Consequently, individuals may become larger without showing improved condition or even exhibit lower condition indices despite increased size. These findings emphasize that body size and body condition capture different aspects of individual fitness and should be interpreted separately.

Factors Influencing Mass

Study site and sex emerged as the main factors affecting body mass. Individuals from Seeschlacht were, on average, heavier than those from Königshaufen, while females had higher body mass than males. These patterns closely mirror the observed differences in snout–vent length (SVL), suggesting that variation in body mass is largely driven by differences in body size rather than by independent effects on mass alone. The effect of sex matches general patterns in amphibians, where females tend to reach higher body mass due to reproductive investment, particularly through egg development.

This contributes to the overall higher mass observed in females compared to males, even when body size differences are moderate. The positive effect of days of year suggests a gradual increase in body mass over the active season. This likely reflects the accumulation of energy reserves, which is used for reproduction or overwintering. Such seasonal dynamics indicate that short-term physiological processes contribute to variation in body mass within years. No significant effects were detected for the year, groundwater level, temperature, or precipitation. This suggests that short-term environmental variation has a comparatively limited influence on body mass when considered independently. Instead, body mass appears to be shaped primarily by more stable factors such as habitat conditions and life-history characteristics. These findings should be considered together with the results for body condition (SMI). While individuals from Seeschlacht were generally heavier than those from Königshaufen, this does not necessarily mean that they were in better energetic condition. Instead, the higher body mass is mainly a result of the larger body size of individuals from Seeschlacht, while body condition was much more similar between the two populations.

Evaluation of Hypotheses

The hypothesis that individuals from the more stable habitat Seeschlacht attain larger body size and higher body mass than those from the dynamic habitat Königshaufen was clearly supported. Individuals from Seeschlacht were larger and heavier throughout the study period, which is in line with the higher apparent survival and older age structure observed in this population.

The hypothesis that individuals from Königshaufen have lower body condition compared to those from Seeschlacht was only partially supported. Although SMI values tended to be slightly higher in Seeschlacht, differences between populations were small and showed considerable overlap. This suggests that body is less strongly influenced by habitat type than initially expected.

Implications for Conservation and Monitoring

The findings indicate that the two populations differ in several demographic and life-history characteristics of *Bombina bombina*, both of which appear ecologically viable under the given environmental conditions. At the same time, they underscore the critical role of habitat characteristics in shaping amphibian life histories, particularly in dynamic floodplain systems. The adaptability of the fire-bellied toad to fluctuating environmental conditions emphasizes the importance of maintaining a network of diverse habitats that includes both stable and temporally variable breeding sites. In the Lobau, however, the loss of natural flood dynamics and ongoing desiccation have promoted vegetation succession, leading to increasing overgrowth of many water bodies and a gradual decline in habitat suitability for *B. bombina*. The artificial supply of Danube water is therefore a key management tool to improve hydrological conditions and maintain suitable breeding habitats. Disturbance processes also contribute to habitat quality. Wild boar create small-scale disturbances that increase habitat heterogeneity, promote open water areas, and slow vegetation overgrowth. This effect aligns with the Intermediate Disturbance Hypothesis (Connell, 1978), which proposes that moderate disturbance increases habitat diversity and creates favourable conditions for a wider range of species and life stages.

In more overgrown areas such as Seeschlacht, additional management measures, including targeted grazing (e.g. with Zackel sheep), could help maintain open breeding habitats by slowing vegetation overgrowth. Furthermore, targeted habitat interventions such as the selective deepening of larger

ponds could improve habitat resilience. Increasing water depth allow access to groundwater during dry periods and provide refuge areas for larvae, thereby reducing the risk of reproductive failure due to premature desiccation. Such measures might become increasingly important under ongoing climate change.

Limitations and Future Directions

Although the statistical analyses provided clear results, several limitations should be acknowledged. The two study sites differ not only in their hydrological characteristics but also potentially in predator communities, resource availability, and genetic or epigenetic structure, all of which may influence demographic patterns. Furthermore, while SVL and body mass are useful proxies for morphological condition, they do not directly measure fitness, as they do not capture reproductive success, survival, or the ability to cope with environmental stress. Several methodological limitations are inherent to field studies in dynamic wetland systems. Water levels and habitat accessibility varied considerably throughout the study period, making complete coverage of all suitable habitats difficult. Unfavorable weather conditions also reduced detectability. Sampling effort varied between years, and fieldwork in 2020 was further limited by restrictions related to the COVID-19 pandemic. These factors introduced variability in detection probability and sampling intensity. Longer observation periods would likely help to reveal environmental effects more clearly. Future studies could benefit from incorporating longer environmental time series and additional ecological variables to improve our understanding of the factors driving population dynamics. Genetic analyses would be particularly valuable for determining whether the two populations function as distinct subpopulations or remain connected through dispersal. Such approaches could also help clarify whether differences in body size and life-history traits are genetically based or primarily reflect phenotypic plasticity in response to local environmental conditions. Taken together, the results indicate that habitat stability fundamentally shapes population dynamics, morphology, and energy allocation in *Bombina bombina*, leading to distinct life-history strategies in stable versus dynamic environments.

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