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„Population dynamics of the European fire-bellied toad, *Bombina bombina*, in Obere Lobau (Donau-Auen National Park, Vienna)"

verfasst von / submitted by

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Abstract

The dynamics of two populations of the European fire-bellied toad, *Bombina bombina*, in the Danube River floodplains of Lobau, Austria, were studied over a period of eight years, from 2015 to 2022. The habitats of the two populations, Seeschlacht and Königshaufen, are characterized by contrasting environmental conditions: Seeschlacht is located behind the Danube flood dike and water levels are relatively stable, while Königshaufen is located on the river side of the dike, resulting in a more dynamic water regime, with strong intra- and interannual changes in water levels. Software supported image identification of photos of fire-bellied toads was used to establish a database and create the capture history of all animals that had been captured and released over the studied period. Capture-recapture models were applied to estimate capture probability, apparent survival, per capita recruitment, and the population size of each population separately. Apparent survival was higher in the more stable Seeschlacht area, while per capita recruitment of adults was higher in the more dynamic Königshaufen area. The population of Königshaufen has witnessed a large drop in 2019, most likely because of unsuccessful reproduction during the previous year, but has been increasing again since then. The population of Seeschlacht was relatively stable but has shown a downwards trend between 2017 and 2022 which may be the result of unfavourable environmental conditions for reproduction in this area.

Zusammenfassung: Die Dynamik von zwei Populationen der Rotbauchunke, *Bombina bombina*, in der Lobau, dem Wiener Teil des Nationalpark Donau-Auen, wurde über einen Zeitraum von acht Jahren, von 2015 bis 2022, untersucht. Die Lebensräume der beiden Populationen, Seeschlacht und Königshaufen, sind durch gegensätzliche Umweltbedingungen gekennzeichnet: Seeschlacht liegt hinter dem Hochwasserdamm und weist relativ stabile Wasserstände auf, während Königshaufen auf der Flussseite liegt, was zu stärkeren Wasserstandsschwankungen innerhalb und zwischen den Jahren führt. Mittels softwaregestützter Bilderkennung von Rotbauchunkenfotos wurde die Fanggeschichte aller im Untersuchungszeitraum registrierten Tiere erstellt. Fang-Wiederfang-Modelle wurden verwendet, um die Fangwahrscheinlichkeit, die lokale Überlebensrate, die Rekrutierungsrate und die Populationsgröße der beiden Populationen zu schätzen. Die lokale Überlebensrate war im stabileren Seeschlacht-Gebiet höher, während die Rekrutierungsrate von adulten Tieren im dynamischeren Königshaufen-Gebiet höher war. Die Königshaufen-Population verzeichnete 2019 einen starken Rückgang, der höchstwahrscheinlich auf eine erfolglose Reproduktion im Vorjahr zurückzuführen ist, hat aber seitdem wieder zugenommen. Die Seeschlacht-Population war relativ stabil, verzeichnete aber seit 2017 einen Abwärtstrend, welcher auf die ungünstigen Bedingungen für die Reproduktion in diesem Gebiet zurückzuführen sein könnte.

Keywords: Amphibia, Bombinatoridae, capture-recapture analysis, population dynamics, software supported image identification.

Introduction

Amphibians are one of the most threatened classes of animals worldwide, witnessing severe declines in populations and facing the increasing risk of extinction of more and more species (Adams et al. 2013, Beebee and Griffiths 2005, Stuart et al. 2004). Currently, around 41% of all known amphibian species are threatened (IUCN 2023). By far the biggest threat to amphibian populations is habitat loss, degradation, and fragmentation due to human activities (Gallant et al. 2007). Other threats include, but are not limited to, climate change, environmental pollution, diseases, and invasive species (Hof et al. 2011). To counteract these negative trends, the study and understanding of the dynamics of amphibian populations is of utmost importance and can help identify early warning signs of declining populations and allow the timely planning and implementation of conservation measures.

The life history of many amphibians is shaped by a complex life cycle, with metamorphosis marking an abrupt ontogenetic change in morphology, physiology, and behaviour, as well as often a change in habitat (Wilbur 1980). Due to their dependence on both terrestrial and aquatic habitats, amphibian populations are especially vulnerable to environmental changes. Environmental stochasticity plays an important role in the shaping of life histories (Tuljapurkar et al. 2009) by directly or indirectly influencing traits such as survival or recruitment, and thus can lead to strong fluctuations of amphibian populations (Fujiwara and Takada 2017). In disturbance-dominated environments such as floodplains, the availability of suitable habitats and spawning grounds depends on water levels. Extreme events such as floods (Cogălniceanu and Miaud 2003) or droughts (Cayuela et al. 2016a) can completely change habitat conditions within a short time.

The European fire-bellied toad, *Bombina bombina*, is a small anuran species that can reach a body-length of around four to five centimetres. It occurs in the lowlands of Central and Eastern Europe and reaches its westernmost distribution area in Austria (Glandt 2015). *Bombina bombina* is a prolonged breeder. Calling activity usually starts at the end of March or in April and lasts until August or September in Austria (Cabela et al. 2001, Grabenhofer 2004). Fire-bellied toads prefer semi-permanent and permanent sun-exposed water bodies with available water vegetation as habitat and breeding grounds (Gollmann et al. 2012).

In Austria, *B. bombina* is mostly distributed in the East, where the floodplains of the Danube and March Rivers, and the wetlands around Lake Neusiedl are its main habitats (Philippi and Gollmann 2014). While *B. bombina* is not threatened on a global scale (Agasyan et al. 2009), it is listed as vulnerable (VU) in the Austrian Red List (Gollmann 2007) and is protected by Annexes II and IV of the Habitats Directive. Major threats for fire-bellied toad populations, especially peripheral ones, include the loss of habitat and water bodies due to river regulations, pollution, and agriculture (Glandt 2015).

The river floodplains of Lobau constitute an important habitat for *B. bombina* populations in Austria. Since the regulations of the Danube River in the 19th century, Lobau has been separated from the mainstream and has lost most of its former natural floodplain dynamics (Schratt-Ehrendorfer and Rotter 1999). While extreme floods can still lead to the inundation of parts of the area, the main hydrological influence comes from the varying groundwater levels shaped by the Danube River (Schiemer et al. 1999). Especially Obere Lobau, the area where this study was conducted, has been decoupled nearly completely from the dynamics of the Danube River (Weigelhofer et al. 2013).

The capture-mark-recapture (CMR) method is an established way of studying the dynamics of animal populations, as it allows the modelling of parameters such as population size, survival, and recruitment from capture histories (Amstrup et al. 2005, Lebreton et al. 1992, 2009, Pollock 2000, Pradel 1996). A variety of studies on the ecology, structure, or dynamics of fire-bellied toad populations from different parts of its distribution area such as Germany (e.g., Buschendorf 1996, Engel 1996, Frenz 2004, Schneeweiss 1996, Vollmer and Große 1999), Denmark (e.g., Briggs 1996, Fog 1996), Romania (e.g., Cogălniceanu and Miaud 2003, 2004, Nicoară and Nicoară 2007) or Latvia (e.g., Pupina and Pupins 2008, 2013), are available. Unfortunately, the number of dedicated long-term studies is still very low. Krappe et al. (2013) conducted a monitoring project of *B. bombina* at two ponds near the village Schlicht in Germany, using the capture-recapture method to estimate the population size for each year. Monitoring took place from 2002 to 2012 for the first pond, and from 2004 to 2012 for the second pond. The estimated population size in both water bodies showed large fluctuations across the years and dropped to zero from 2004 to 2007 in one of the ponds when it had completely dried out. The shifts in population size were attributed to the varying water levels of both ponds, climatic conditions, predation, and food availability among other factors. Temporal emigration to other water bodies in the surrounding areas may have also occurred when environmental conditions were unsuitable at the two ponds.

In Austria, thorough investigations of populations in many of the fire-bellied toad's distribution areas are still missing (Schedl 2005). Most available population studies are limited to a few select areas, such as a floodplain of the March River in eastern Austria (Seidel 2012), Neusiedler See-Seewinkel National Park (Grabenhofer 2004, Grillitsch and Grillitsch 1984) or Lobau (Philippi 2013, Philippi and Gollmann 2014) and mostly do not include long-term data. Kogoj (1997) studied the population dynamics of *B. bombina* and other amphibian species at an artificial pond on the Danube Island in Vienna for multiple years. The population was relatively stable, but its size still decreased over the studied period. Potential reasons for the decline include succession processes reducing the quality of the pond, a higher risk of predation, interspecific competition, or the loss of suitable places for hibernation.

The status of the two fire-bellied toad populations in Lobau that are the topic of this study was assessed using data from 2008 (Philippi and Gollmann 2014). The capture-recapture method was applied to estimate the population size for both areas. Population size was calculated at 650 individuals between May and June 2008 at Königshaufen and 115 individuals between April and May 2008 in Seeschlacht. Despite being a dry year, reproductive success was proven in 2007, in 2008 the number of metamorphs exceeded thousands at Königshaufen. Due to flooding in 2009, fish were introduced into several water bodies which had a negative impact on metamorphic success. Philippi (2013) remarks that long-term monitoring at multiple spawning sites will be necessary to estimate the probability of survival and to study and assess population trends to make informed decisions about potential future protection and conservation measures for *B. bombina* in Lobau.

The aim of this study was to compare the two above-mentioned populations of European fire-bellied toads in contrasting environments of Lobau and interpret differences between them in the context of the different predominant habitat conditions of each population using data that had been collected over a period of eight years, during the spring and summer seasons of 2015 to 2022. Software supported image identification of photos of fire-bellied toads was used to establish a database and create the capture histories of all individuals that had been captured and released over the studied period. Capture-recapture models were applied to calculate the probability of survival and recruitment for both populations separately, and to estimate the population sizes.
It was expected that the population in the more stable environment of Seeschlacht would show higher probability of adult survival but lower recruitment rates, whereas the population in the more dynamic environment of Königshaufen would have higher recruitment but also lower probability of survival for adult individuals.
The findings of this study will be compared to the results of similar studies about the population dynamics of *B. bombina* and other amphibian species and are intended to provide information about the conservation status of both populations.

Material and methods

Study area

The study was conducted in the river floodplains of Lobau on the northern bank of the Danube River to the east of the city of Vienna, Austria (Fig. 1). Lobau is the westernmost part of the Donau-Auen National Park and covers an area of around 2300 ha. It is characterized by a continental sub-Pannonic climate with annual precipitation between 500 and 700 mm and annual mean temperatures of around 10 °C. Across the study years 2015 to 2022, annual precipitation ranged from 392 mm in 2022 to 647 mm in 2020 (mean across all eight years: 535.25 mm), annual mean temperature ranged from 10.87 °C in 2021 to 12.17 °C in 2018 (mean across all eight years: 11.64 °C) (data were obtained from a weather station in Groß-Enzersdorf; www.zamg.ac.at/).

As a result of major regulations of the Danube River in the 19^{th} century, the floodplains of Lobau have been separated nearly completely from the mainstream, and the dynamic erosion and accumulation processes of natural floodplains have largely been lost (Schratt-Ehrendorfer and Rotter 1999). Since then, groundwater levels have been steadily declining (Weigelhofer et al. 2005) and terrestrialization and succession processes have changed the area towards a shallow lake-like system (Baart et al. 2013). Water level fluctuations of backwaters are low, as the main hydrological connection to the river is via groundwater (Schiemer et al. 1999).

Lobau is separated into two areas: The downstream part, Untere Lobau, still receives flood waters via the Schönauer Schlitz, an opening in the flood dike, and is therefore still subject to more dynamic environmental conditions. In contrast, the upstream part Obere Lobau where the two studied *B. bombina* populations are located, is completely disconnected from direct flood effects (Weigelhofer et al. 2011). Terrestrialization processes are still ongoing today and especially affect many of the smaller water bodies found in this area. Over a period of 56 years, 27 ha of water bodies and wetlands have been lost (Reckendorfer et al. 2013). The reduced dynamics also have led to the development of extended reed communities (Weigelhofer et al. 2011).

To improve the hydrological situation of Obere Lobau, a water enhancement scheme in the form of a controlled surface water supply along a chain of backwaters was initiated in 2001 (Funk et al. 2009). Between March and October, water is channelled from the Alte and Neue Donau to Oberes Mühlwasser and from there to Obere Lobau. During the first four years, the maximum discharge was restricted to 0.5 $m^3 s^{-1}$, but the limit was later increased to 1.5 $m^3 s^{-1}$ (Weigelhofer et al. 2013). These measures led to a significant increase and stabilization of surface and groundwater levels, improved the trophic conditions of the backwaters (Weigelhofer et al. 2011), and had positive effects on organisms such as dragonflies and molluscs (Funk et al. 2009).

Study sites

Data were collected at two sites of *Bombina bombina* populations in Obere Lobau, the upstream part of Lobau that covers an area of around 540 ha (Fig. 1). The study sites differ in number and size of available water bodies, environmental conditions, and pond hydroperiod, and are located on the opposite sides of the OMV central fuel depot, which serves as a physical barrier between them. Numeration and some information about characteristics of water bodies were adopted from Schedl et al. (2009).

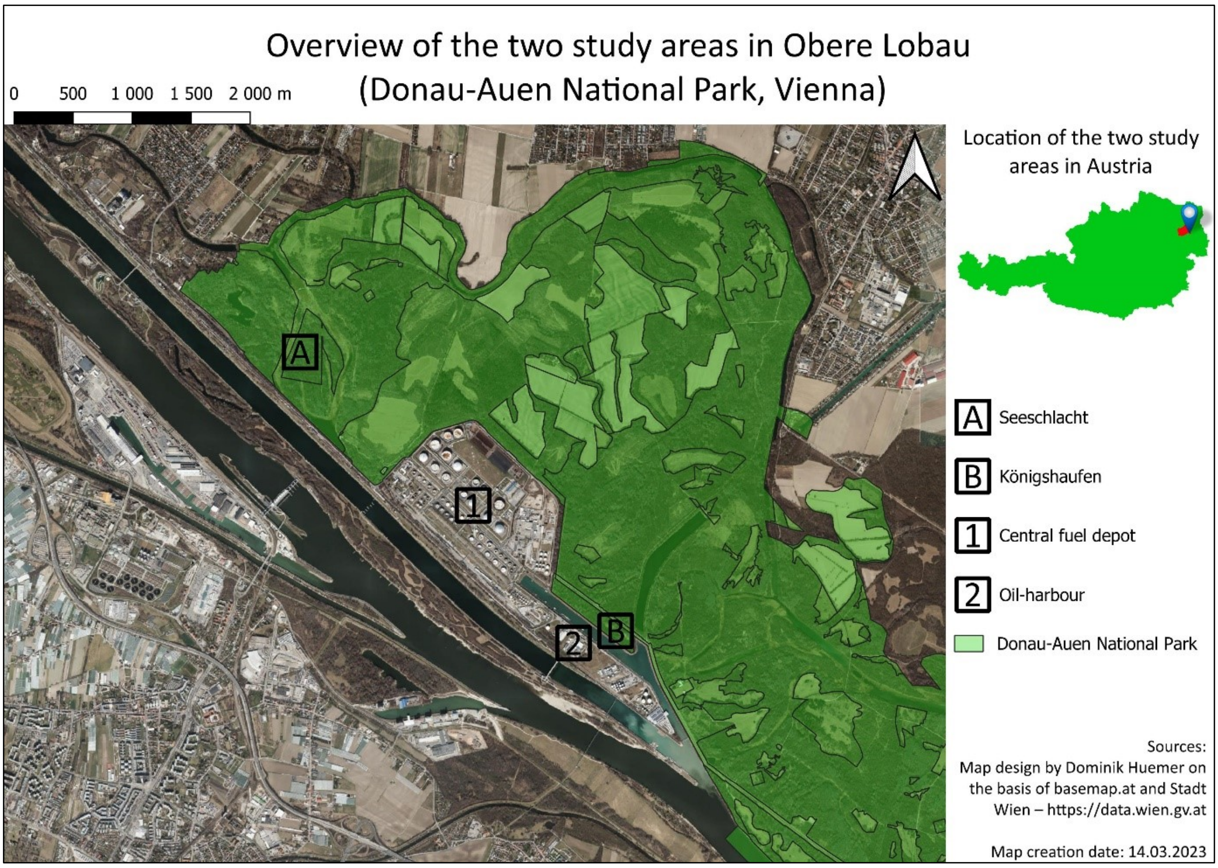

Fig. 1: Overview of the two study areas in Obere Lobau: (A) Seeschlacht, (B) Königshaufen, (1) central fuel depot, (2) Lobau oil-harbour. The green shading shows the Donau-Auen National Park in Vienna. The map was created with QGIS (2023) (v3.30.0; www.qgis.org/).

The first study site is located to the north-west of the central fuel depot and will be referred to as "Seeschlacht" (Fig. 2, Fig. 3). Seeschlacht consists of several smaller and, depending on the water level, medium-sized water bodies spread across a wider area. Most of the small water bodies are water-filled bomb craters located both inside and outside of the forest. Bomb craters within the forest were shaded by the surrounding trees, free of any vegetation (some were covered by duckweeds, *Lemna* sp.), and were often covered with leaves and dead branches. Some bomb craters outside of the forest (mainly water bodies 6 and 7) were densely covered with thick reeds (*Phragmites* sp.).

The medium-sized water bodies consist of a network of partially interconnected water channels on open areas outside of the forest that can become completely submerged when water levels are high enough. As the seasons progressed these areas became more and more overgrown with reeds (*Phragmites* sp.).

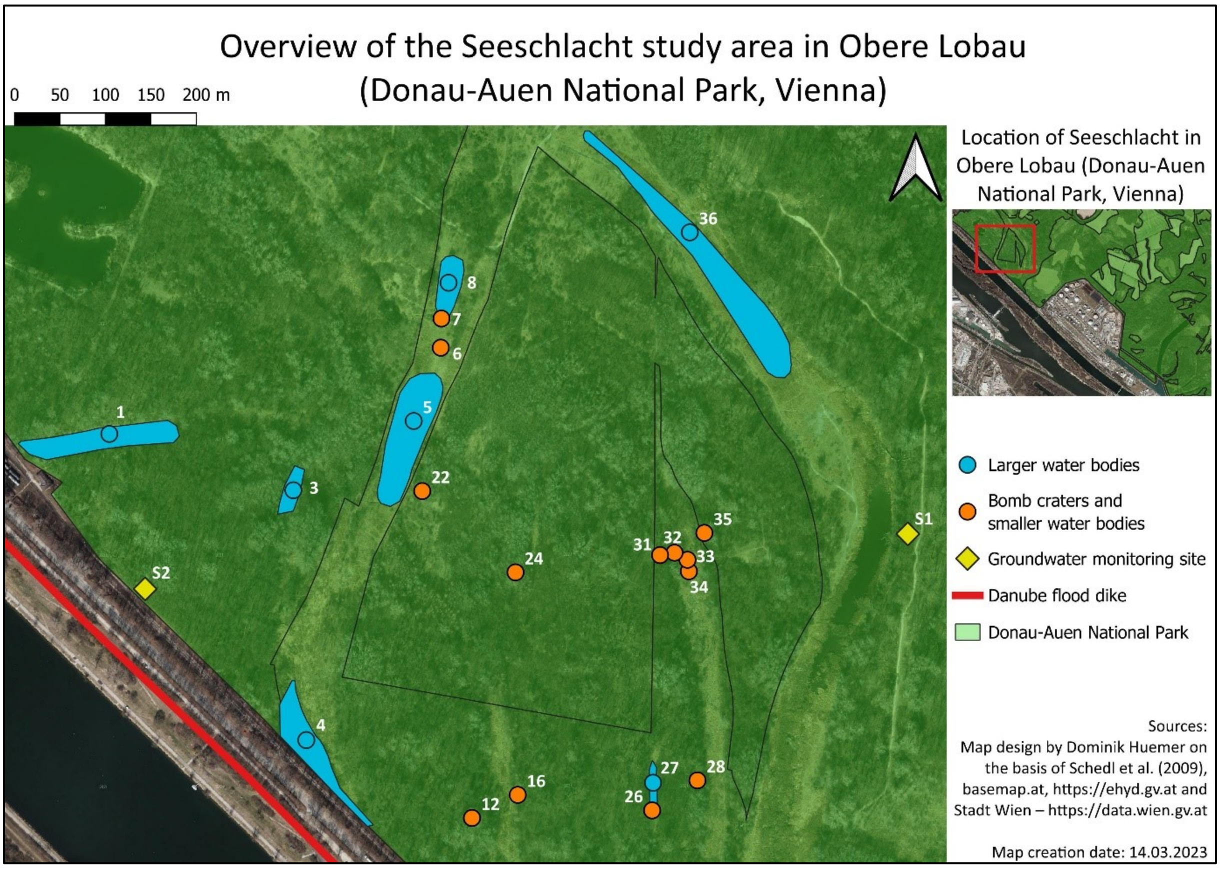

Fig. 2: Overview of the Seeschlacht study area showing all water bodies where fire-bellied toads were captured between 2015 and 2022. The map was created with QGIS (2023) (v3.30.0; www.qgis.org/).

Seeschlacht is located behind the Danube flood dike and is therefore not much influenced by the varying water levels of the Danube River. As a result, environmental conditions are relatively stable and predictable due to mostly constant or only slightly fluctuating water levels. The study site Seeschlacht was classified as "stable".

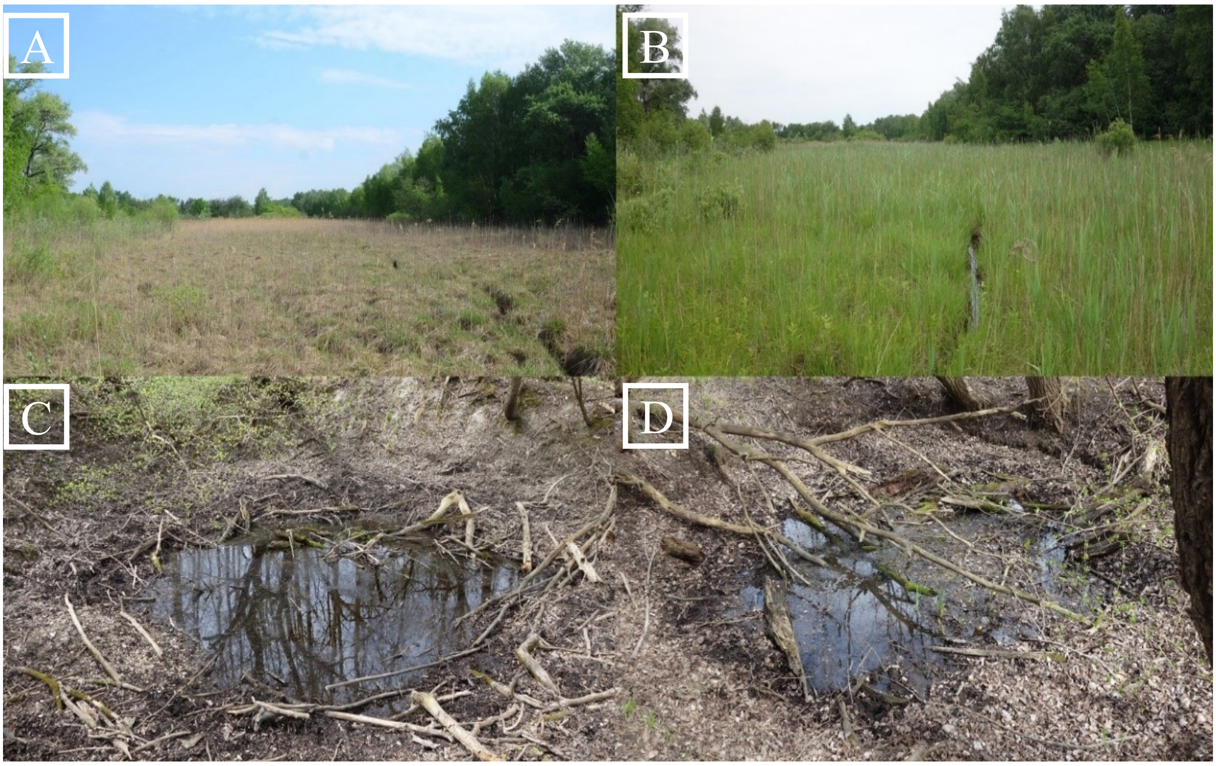

Fig. 3: Selection of water bodies in Seeschlacht. (A) and (B) show one of the medium-sized water bodies (number 5 in Fig. 2) at two different dates in 2018: (A) on April 24 and (B) on May 30. The area became rapidly covered by reeds (*Phragmites* sp.) as the season progressed. (C) and (D) show two different bomb craters within the forest on April 11, 2018.

The second study site is located to the north-east of the oil-harbour and will be referred to as "Königshaufen" (Fig. 4, Fig. 5). The area consists of two medium- to larger sized semipermanent ponds (water bodies number 62 and 63) in close vicinity to each other, surrounded by trees. The ponds are separated by an embankment overgrown with bushes and trees. Both ponds are nearly fully exposed to the sun, only the edges are shadowed by the surrounding trees at different times of the day. A lot of dead wood was present in both ponds. If water levels were not too high early in the season, pond number 62 could become more and more overgrown with sedges (*Carex* sp.), while pond number 63 did not develop nearly as much vegetation.

Königshaufen is the only area in Obere Lobau that is not located behind the Danube flood dike and is therefore directly influenced by the changing water levels of the Danube River, resulting in a more dynamic and unpredictable environment, with strong changes in water levels throughout the season and across the years being possible (Fig. 7). At times the ponds can completely dry out. The study site Königshaufen was classified as "variable".

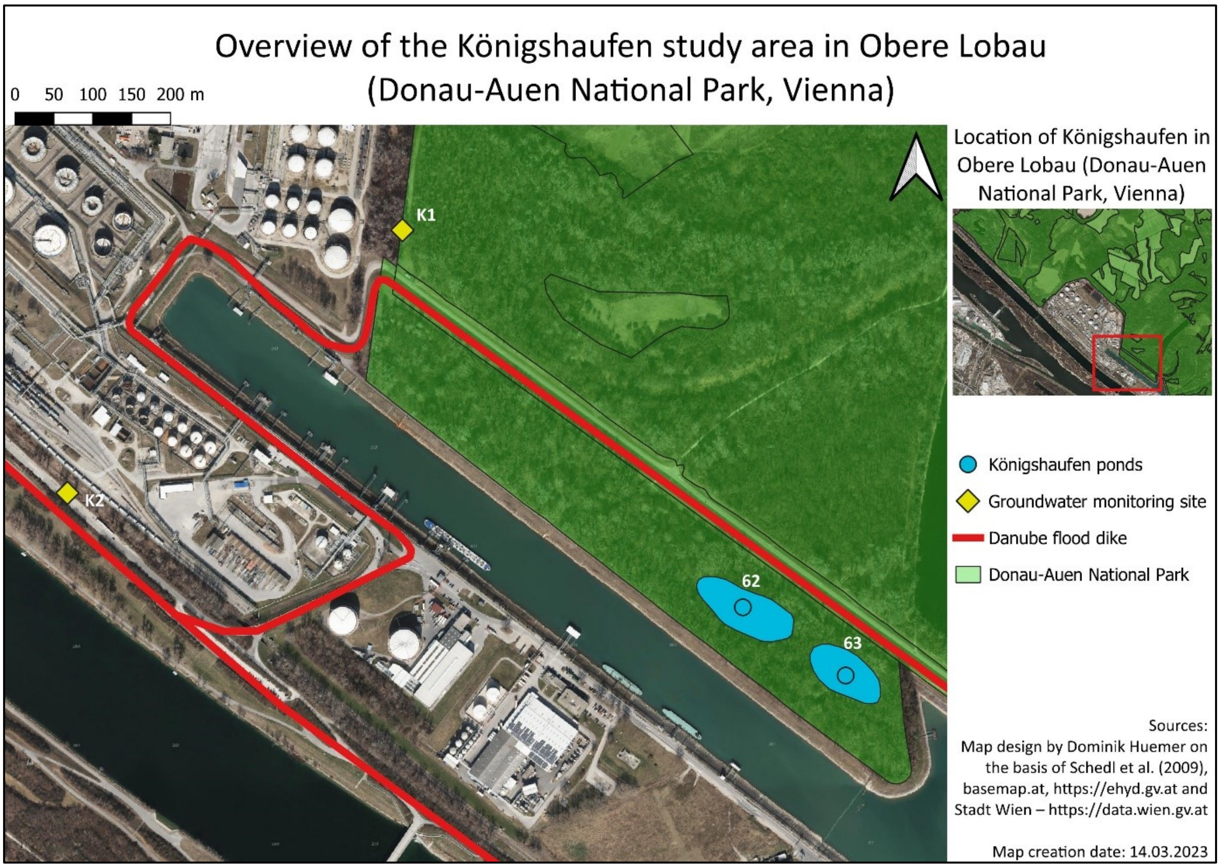

Fig. 4: Overview of the Königshaufen study area. The two ponds are located on the river side of the Danube flood dike and are directly influenced by the Danube. The map was created with QGIS (2023) (v3.30.0; www.qgis.org/).

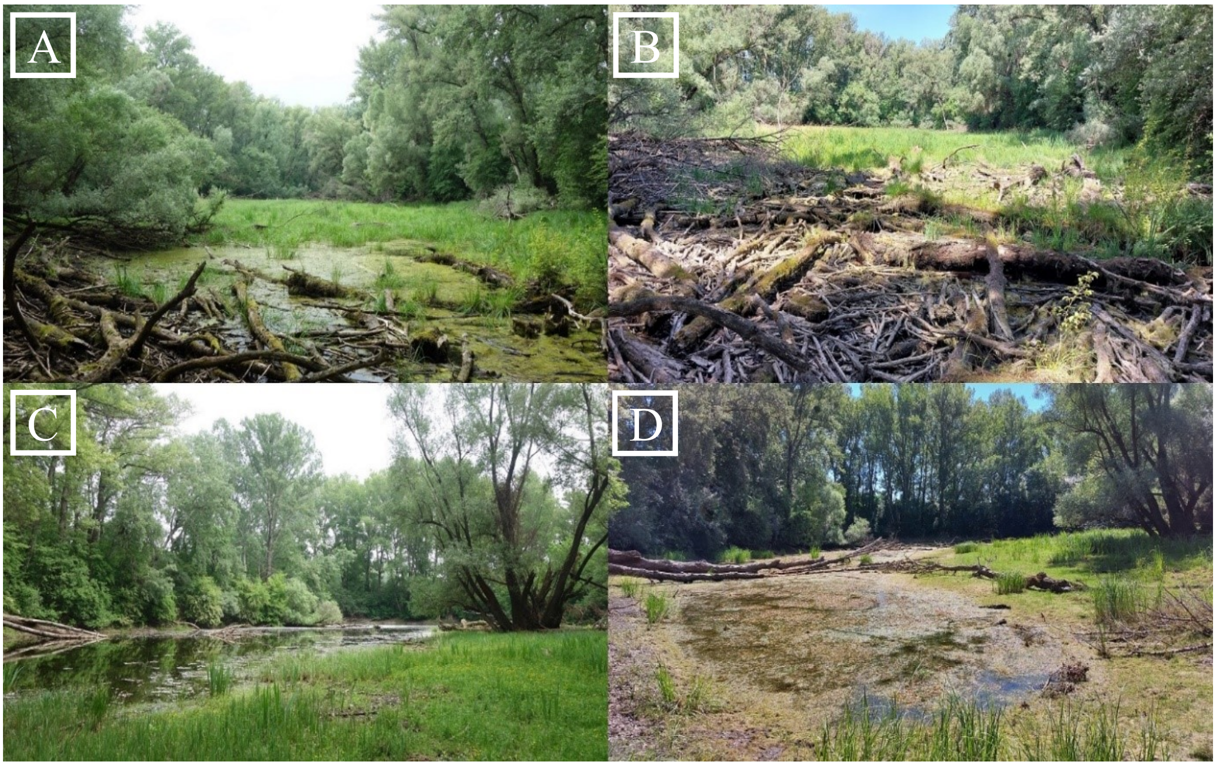

Fig. 5: The two ponds of Königshaufen. (A) and (B) show pond number 62 during two different years: (A) on June 7, 2018, and (B) on July 14, 2022. (C) and (D) show pond number 63 during two different years: (C) on May 4, 2018, and (D) on July 14, 2022.

Habitat types from Annex I of the Habitats Directive (see Ellmauer and Traxler 2000) in Obere Lobau are shown in Fig. 6. The dominant habitat type was riparian mixed forest (91F0), the two Königshaufen ponds were surrounded by a patch of alluvial forest (91E0*). Most water bodies were classified as natural eutrophic lakes with Magnopotamion or Hydrocharition -type vegetation (3150). The remaining habitat types consisted of smaller, mostly fragmented patches spread across Obere Lobau: semi-natural dry grasslands and scrubland facies on calcareous substrates (6210*), sub-Pannonic steppic grasslands (6240*), lowland hay meadows (6510), and alkaline fens (7230).

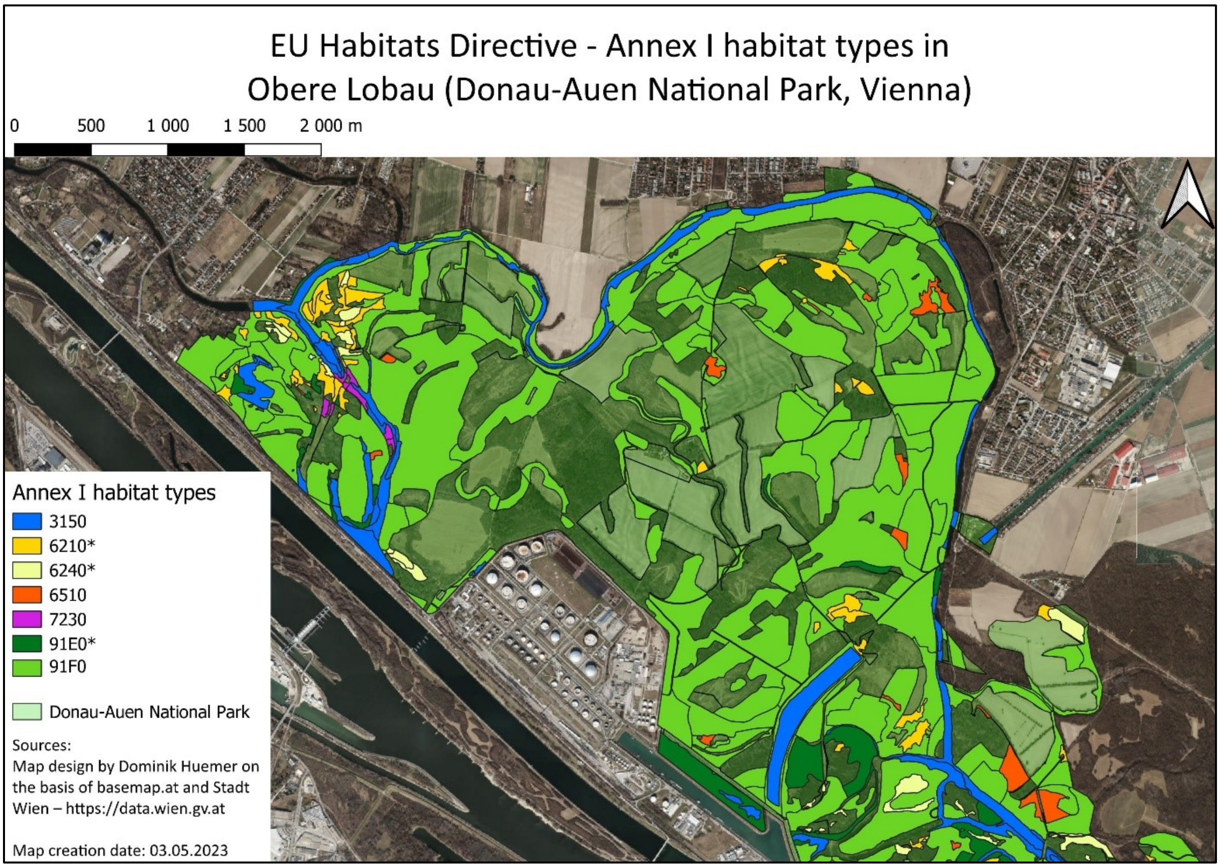

Fig. 6: Overview of the habitat types from Annex I of the Habitats Directive in Obere Lobau: 3150 (Natural eutrophic lakes with Magnopotamion or Hydrocharition -type vegetation), 6210* (Semi-natural dry grasslands and scrubland facies on calcareous substrates), 6240* (Sub-Pannonic steppic grasslands), 6510 (Lowland hay meadows), 7230 (Alkaline fens), 91E0* (Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior*), and 91F0 (Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*, *Fraxinus excelsior* or *Fraxinus angustifolia*). Asterisks indicate priority habitat types. The map was created with QGIS (2023) (v3.30.0; www.qgis.org/).

Groundwater levels

To illustrate the contrasting environmental conditions between Königshaufen and Seeschlacht, the groundwater levels of four monitoring sites for the months March to August of each study year are shown in Fig. 7. The chosen monitoring sites, two per study area, were located closest to the water bodies of each area (Fig. 2, Fig. 4). Monitoring sites S1 (341578 Wien 22, Bl 22-202; 155.45 m a.s.l.) and S2 (313015 Wien 22, Br 22- 17; 156.36 m a.s.l.) in Seeschlacht are located approximately 220 and 170 meters from the closest water body respectively, monitoring sites K1 (333401 Wien 22, Bl 22-174; 154.28 m a.s.l.) and K2 (350215 Wien 22, Bl 22-242; 157.61 m a.s.l.) at Königshaufen are located approximately 630 and 860 meters from pond number 62 respectively.

For the first four study years, monthly mean groundwater levels were available for all four monitoring sites, from 2019 to 2022 only for S2 and K2 (for April 2021, only data of two days were available for K2). After 2018, depicted values of S1 show groundwater levels of only one day per month, for some months no data were available at all. For K1, groundwater levels of one to four days were available for each month, mean values were calculated for all months with data of two or more days.

To show the high correlation between groundwater levels at Königshaufen and water levels of the Danube River, monthly mean water levels of the Danube River from monitoring site Donaukanalmündung (148.82 m a.s.l.; N 48° 09' 56'', E 16° 29' 47'') are also included in Fig. 7.

Groundwater data for the years 2015 to 2018 were provided by the Bundesministerium für Land- und Forstwirtschaft, Regionen und Wasserwirtschaft (BML; www.ehyd.gv.at/), for the years 2019 to 2022 by Magistratsabteilung 45 (MA 45; Wiener Gewässer). Danube River water levels were provided by via donau (Österreichische Wasserstraßen-GmbH; www.viadonau.org/).

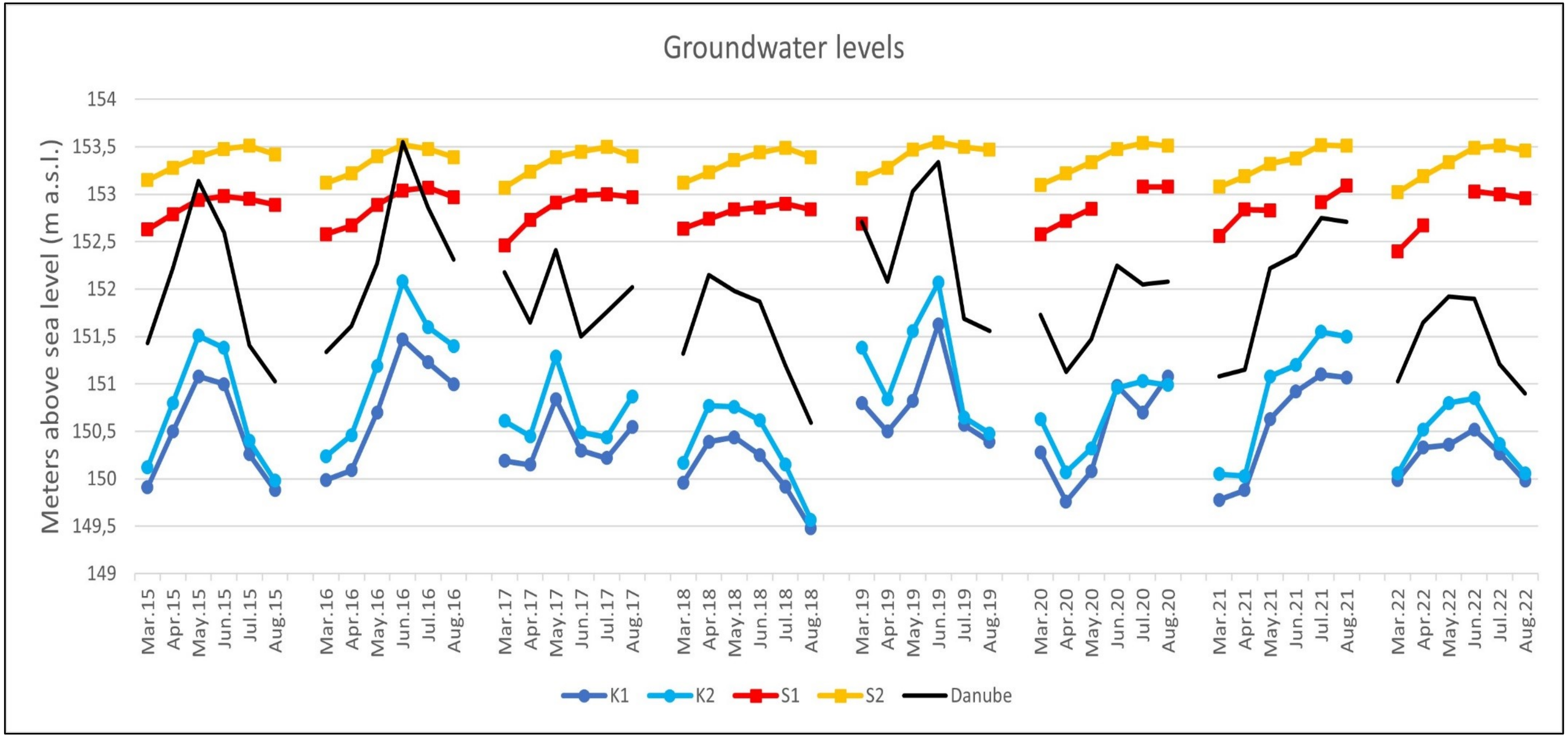

Fig. 7: Groundwater levels of four groundwater monitoring sites in Obere Lobau for the months March to August between 2015 and 2022. Monitoring sites K1 and K2 are located at Königshaufen, S1 and S2 in Seeschlacht. Monthly mean groundwater levels are shown for all four monitoring sites from 2015 to 2018. Between 2019 and 2022, monthly mean groundwater levels are only depicted for S2 and K2 (for April 2021, only data of two days were available for K2). After 2018, S1 shows the groundwater levels of one day per month, for some months no data were available. K1 shows the (mean) groundwater levels of one to four days per month (mean values were calculated for all months with data of two or more days). Monthly mean water levels of the Danube River (black line) from monitoring site Donaukanalmündung are also included.

Data collection

Data collection took place over a period of eight years during the spring and summer seasons of 2015 to 2022. Both study sites were visited semi-regularly multiple times per year, usually starting at the end of March or in April until July or August (for exact dates see Tables A1 through A8 in supplementary material). In 2015 both areas were visited for the last time in June, in 2020 sampling did not start until June. Field trips took place during the day and lasted for several hours depending on weather conditions and sampling effort. Königshaufen was visited a total of 45 times, Seeschlacht was visited a total of 42 times (Table 1).

Table 1: Overview of the number of sampling occasions per year and study area.

Year	Study site	# of times visited
2015	Königshaufen	4
	Seeschlacht	4
2016	Königshaufen	5
	Seeschlacht	5
2017	Königshaufen	5
	Seeschlacht	4
2018	Königshaufen	6
	Seeschlacht	5
2019	Königshaufen	7
	Seeschlacht	6
2020	Königshaufen	4
	Seeschlacht	5
2021	Königshaufen	7
	Seeschlacht	6
2022	Königshaufen	7
	Seeschlacht	7
Total	Königshaufen	45
	Seeschlacht	42

Fire-bellied toads were captured on sight by hand or with a dip net and put into plastic boxes with a small amount of water inside. Water bodies were sampled individually, larger ones were split into two halves that were sampled one after the other. The water bodies where animals were captured differed from year to year in Seeschlacht (Table 2). Water bodies that were not carrying any water or where not a single toad was found were excluded from sampling for the rest of the respective year.

Number and location of each capture event were noted. Photos of the individually distinctive colour patterns on the ventral side of the captured animals' bodies were taken with a digital camera (Fig. 8). These patterns are unique for each animal and can be used to recognize and identify individual fire-bellied toads (Gollmann and Gollmann 2011). Snout-vent-length (SVL) was measured with plastic callipers and body mass was measured using a portable digital gram scale. If a male and a female individual were found in amplexus, they were only photographed, and no measurements were taken.

Fig. 8: Photo of a European fire-bellied toad's ventral side. The colour patterns on its belly and throat are unique and can be used to identify individual animals. The photo was taken on August 3, 2022, in Seeschlacht.

All captured toads were assigned to one of the three different age-classes "metamorphs", "juveniles" and "adults". Individuals that were captured between metamorphosis and their first hibernation were classified as "metamorphs" (Briggs 1996). Individuals that were smaller than 35 mm and did not show any external secondary sexual characteristics (see below) were classified as "juveniles". Individuals with a snout-vent-length of 35 mm and above, and individuals that were smaller than 35 mm but already had visible secondary sexual characteristics were classified as "adults".

Table 2: List of all water bodies where fire-bellied toads were captured between 2015 and 2022. Water bodies number 1 through 36 are in Seeschlacht, number 62 and 63 are the two Königshaufen ponds. Water bodies where at least one fire-bellied toad was captured during a respective year are marked with "x". Water bodies where not a single individual was captured over the study period were excluded from the list. Numeration of water bodies was adopted from Schedl et al. (2009).

Water body	2015	2016	2017	2018	2019	2020	2021	2022
1	x							
3		x		x		x	x	x
4	x	x		x				
5	x	x	x	x	x	x	x	x
6		x	x	x	x		x	x
7	x	x	x	x	x	x	x	x
8					x	x		x
12		x						
16		x						
22	x	x	x	x	x	x	x	x
24						x	x	x
26		x		x				x
27			x		x			
28		x	x					
31		x		x	x	x	x	x
32		x		x	x	x	x	x
33			x	x	x		x	x
34		x	x		x	x	x	x
35		x		x	x	x	x	x
36	x	x	x	x	x	x		x
62	x	x	x	x	x	x	x	x
63	x	x	x	x	x	x	x	x

All adult *Bombina bombina* individuals were sexed in the field based on whether they showed any secondary sexual characteristics or not. Males were distinguished from females by the dark nuptial pads on their arms and fingers which are visible during mating season, and by their internal vocal sacs that can be seen when they are vocalizing (Glandt 2015). Male individuals also often emit release calls when they are held in hand, a behaviour which can also be observed from females, albeit less frequently, and female release calls sound slightly different from male ones (Gollmann et al. 2009). Adult individuals without any external secondary sexual characteristics were classified as females. All fire-bellied toads were released unharmed at their respective sites of capture.

The photos and additional data of each capture event from 2015 to 2022 were collected by participants of a field course at the University of Vienna. I took part in data collection myself during the spring and summer seasons of 2018 and 2020.

All photos were assembled into individual folders sorted by date and area of capture and were then renamed after the following scheme: "CET_##### YYYY-MM-DD O/B". "CET", stands for "Capture Event Total" and shows the order in which the photos were taken, followed by the date and area of the capture event, "O" stands for "Oilport" (= Königshaufen), "B" for "Backwater" (= Seeschlacht). The data from field work were added to a Microsoft Excel file (Table 3).

Software supported image identification

All photos were edited using the freely available open-source graphics software GIMP (2022). If necessary, the photos were rotated first so that the animal's snout was at the bottom and its cloaca was at the top. Then any unnecessary background was reduced to a minimum so only the ventral side of the fire-bellied toad's body, including its arms, was left (Fig. 9).

Fig. 9: Example of a photo before (A) and after (B) editing.

Fire-bellied toads were identified using the software IBEIS (**I**mage **B**ased **E**cological **I**nformation **S**ystem) (Crall 2021), a software that compares images to detect and match similar patterns between them to identify individual animals. IBEIS only runs on Linux operating systems, to use IBEIS on a Windows operating system, the freely available software VirtualBox (2021) was used.

The edited photos were added to IBEIS one folder at a time. For every folder a new image set was created in IBEIS, containing all photos from its respective date and study area (Fig. 10). The image set "All Images" contained all images that had been added to the database so far, the image set

“Exemplars” contained all photos that had already been compared with one another. Newly added images were compared to all other images that had been marked as “Exemplars”.

When clicking on one of the image sets, a tab called “Image Table” showing a list of all photo files it contains opens to the right (Fig. 10). The checkboxes in the column “Detection Reviewed” were checked to verify all photos correctly showed fire-bellied toads. Next, all files within the image set were selected and with a click of the right mouse button the option “Add annotations from entire images” was selected. In this case, the entire photo will be used for comparison as opposed to just a selected part of the photo. A new tab called “Annotations Table” was created, containing the sections of all photos that were going to be compared (Fig. 11). The column “Species” was set to “bombina_bombina” for all entries.

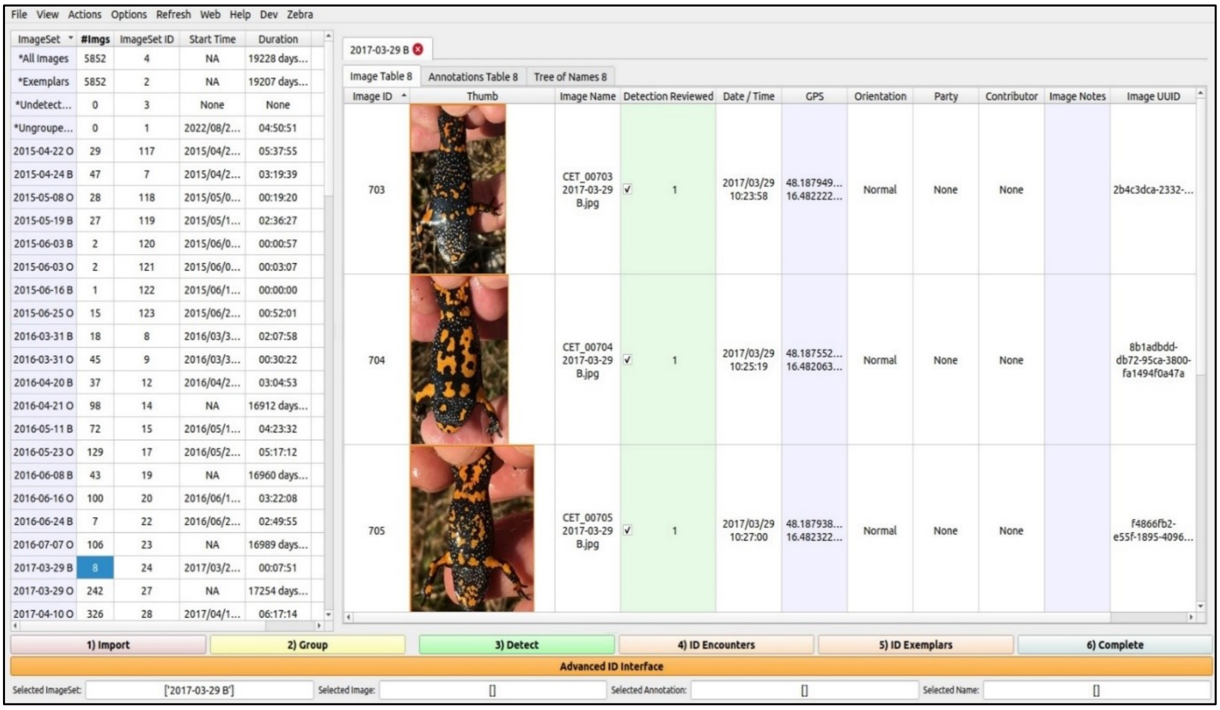

Fig. 10: Screenshot of the user interface of IBEIS. Image sets and the number of respective images within them can be seen on the left, the image table of one of the image sets can be seen on the right.

From the “Actions” menu the command “Query: vs exemplars” was selected. IBEIS then compares all images that are not marked as “Exemplars” to all other images that are already marked as such. Comparison runs could take between a few seconds and several minutes or more, depending on the number of photos that are compared to one another and on the hardware of the PC IBEIS is running on. In a few cases the command “Query: Intra Occurrence” was used first. In this case IBEIS compares all photos within a single image set to one another to potentially identify animals that had been captured twice or more often in the same sampling session.

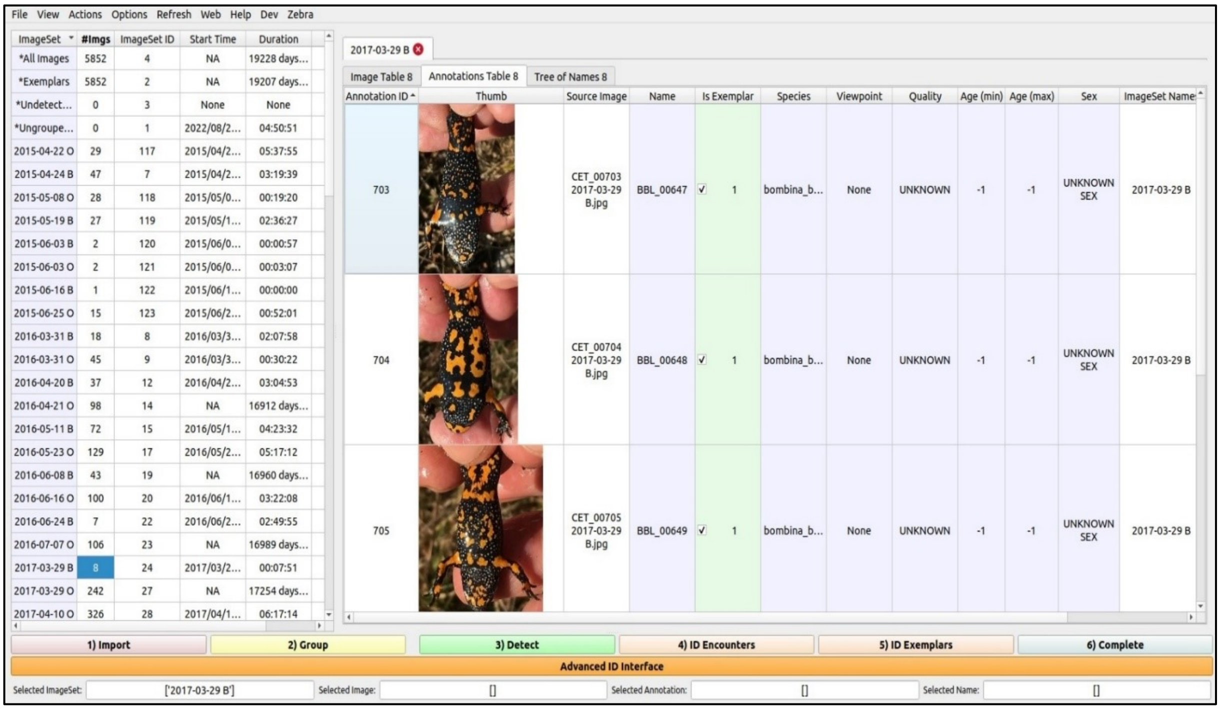

Fig. 11: Screenshot of the user interface of IBEIS. Image sets and the number of respective images within them can be seen on the left, the annotations table of one of the image sets can be seen on the right.

After the comparison of an image set, IBEIS creates a list of all photos that were compared to one another, sorted by their score (Fig. 12). The higher the score of a photo pair, the more similarities IBEIS found between the two images. Starting from the highest score, the individual photo pairs were then manually examined one after the other to check whether there were any recaptures or not. As a rule of thumb, the number of photo pairs that were examined was at least twice as high as the number of photos of the image set that had been compared, e.g. if the new image set that had been compared contained a hundred photos, the first two hundred photo pairs were checked for recaptures.

If the photos of a pair showed the same *Bombina bombina* individual, the entry was marked as "Positive" in the "Matched" column by pressing the "T" button. The ID of the exemplar photo ("name") is then automatically assigned to the query one ("qname"), so both photos now have the same ID. The IDs were named "BBL_#####" which stands for "Bombina Bombina Lobau", followed by the number of the respective individual. All other photos that had not been identified as recaptures were given a new ID, starting from "BBL_00001". Afterwards, the checkboxes in the "Is Exemplar" column of the annotations tab were checked for all entries of the image set that had been compared to include them in subsequent comparison runs.

Lastly, after each comparison run done with IBEIS, the results were compared with the findings from the university field course to identify potential recaptures within a year which might have been missed by IBEIS. Each year the participants of the field course were looking for recaptures among the photos that had been taken during that respective year by manually comparing the photos on a PC. However, due to time constraints, only a part of the photos was compared during most of the years. In this manner, a few more recaptures were identified that would have been missed otherwise.

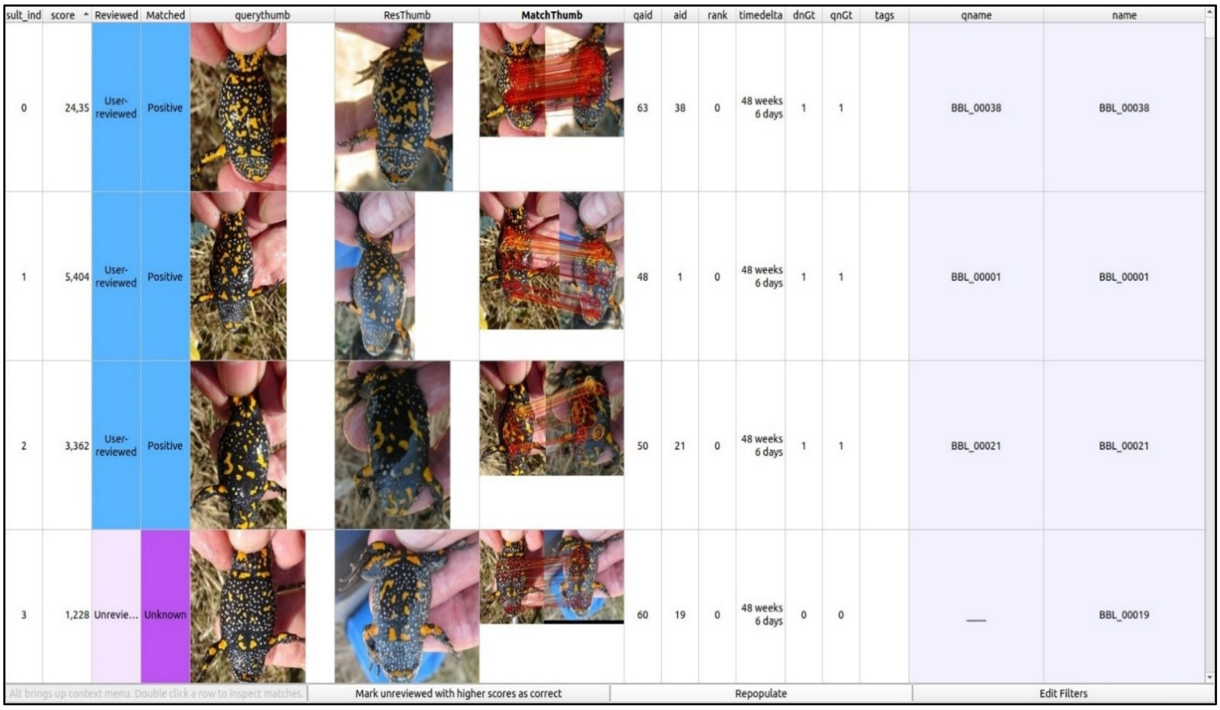

Fig. 12: Screenshot of the top four results of the comparison of an image set with IBEIS. Photo pairs that were compared to one another are sorted by their respective score. The higher the score the more similarities IBEIS found between the two photos of a pair.

The results of the comparisons done with IBEIS were added to the Microsoft Excel file containing all data from field work (Table 3). The IDs (“qname” in Fig. 12) of all individuals identified as recaptures were added to the “id” column of their respective entries. The CET-numbers of the exemplar photos of all matching photo pairs were noted in the column “IBEIS-match” of the respective query photos to record which photos were matched with each other. In cases of multiple positive matches for the same query photo, only the CET-number of the photo with the highest score was noted. Then all other individuals that had not been identified as recaptures were given a new ID in IBEIS (“Name” column of the annotations tab) which were then added to Excel (“id” column). The column “first-recap” was set to “first” for all animals that were captured for the first time, and to “recap” for all animals that had already been captured before. All photos without any positive matches were noted as “none” in the column “IBEIS-match”. If individual fire-bellied toads were recaptured, all entries of that individual (also the one from its first capture) were set to “yes” in the column “ever recaptured” and to “no” if the individual had only been captured once so far.

Lastly, two columns containing information about the sex of each individual were added after image comparison. The first new column, “sex_tagesaktuell”, contains the corrected sex classifications after reviewing the photos of each *Bombina bombina* individual, which was done by Daniel Philippi from the University of Vienna. With the information obtained from image identification, the sex of fire-bellied toads was also retroactively assigned to all juvenile animals that had been recaptured as adults and added to the second new column "sexlabel_final".

The entries of all recaptured animals were reviewed by filtering the column "ever recaptured" by "yes" and sorting them by their IDs to make sure that the sex of an individual did not change from male to female or vice versa, and that adult individuals were not wrongly classified as juveniles on later capture occasions.

Table 3: Content and description of the Microsoft Excel file containing all data from field work and image comparison.

Column name	Column description
exclude from dataset	Entries of fire-bellied toads that are to be excluded from different kinds of data analysis due to missing data; "no" = not to be excluded, "if morpho" = morphometric data are missing, "if MRR" = photo is missing, "meta" = metamorph, "DF" = individual was captured twice on the same sampling occasion;
eventtotal	Consecutive number of capture events over the whole study period
eventyear	Consecutive number of capture events within a year
eventday	Consecutive number of capture events within a day
year	Year the capture event took place in
month	Month the capture event took place in
day_in_year	Number of the day of the year the capture event took place in
days_from_first_day	Number of days that had passed since the first day of sampling
date	Date of the capture event
area	General sampling area
location	Number of the water body the capture event took place in
details_location	More detailed information about the location the capture event took place in
CET	**C**apture **E**vent **T**otal; Consecutive number of the capture event
id	Unique ID of every fire-bellied toad individual (recaptures get the same ID as the first capture)
first-recap	Information on whether the fire-bellied toad was captured for the first time or had already been captured before
IBEIS-match	CET-number of the photo the entry was matched with in IBEIS in case of a recapture
Image_Quality	Image quality of the source photo
NotizenIBEISDominik	Notes and comments from image comparison with IBEIS
ever recaptured	Information on whether the fire-bellied toad was ever recaptured
agelabel_final	Age class of the fire-bellied toad
sexlabel_final	Retroactively assigned sex of juvenile fire-bellied toads that had been recaptured as adults
sex_tagesaktuell	Reviewed and corrected sex classification of the fire-bellied toad
sexlabel_field	Sex classification during field work
svl	Snout-vent-length of the fire-bellied toad
mass	Body mass of the fire-bellied toad
notes	Notes and comments about the fire-bellied toad
camera	Owner of the digital camera the photos were taken with
urspr.ID	Initial ID of the fire-bellied toad
originalfilename	Original file name of the source photo

Statistical analysis

All statistical analyses were made in software R (v4.2.0; R Core Team 2022). To access all relevant data from Excel, the package readxl (Wickham and Bryan 2023) was used. The package openCR (v2.2; Efford 2022) was used for population statistics. Fire-bellied toads without a photo, the second capture event of individuals that had been captured twice on the same sampling occasion, and metamorphs ("if MRR", "DF" and "meta" in the "exclude from dataset" column in Excel respectively) were excluded from statistical analysis. The capture histories of all *Bombina bombina* individuals were created with the "make.capthist" function in openCR. The factor "sex" was added as an individual covariate (information about sex was taken from the "sex_tagesaktuell" column in Excel). Two sets of capture histories were made for each study area, one including toads of both age-classes (juveniles and adults), and one including only adult toads. Data follow a "robust design", where primary sampling sessions (years) consist of secondary sessions (sessions within each year), and populations are assumed to be closed within, and open between primary sessions (Efford 2022, Kendall et al. 1995). The function "openCR.fit" was used to estimate capture probability (p), apparent survival (φ) and per capita recruitment rate (f) using the non-spatial Jolly-Seber-Schwarz-Arnason model for open populations with conditional likelihood and per capita recruitment parameterization (type "JSSAfCL" in openCR) (Efford 2022, Pledger et al. 2010). Four separate full models were created, one for each set of capture histories (Königshaufen all animals, Seeschlacht all animals, Königshaufen adults only, and Seeschlacht adults only). Individual models were tested within those full models. Parameter combinations were the same for all four full models. Capture probability (p) was modelled as constant, varying between sexes, and varying through time with a non-continuous time effect. Apparent survival (φ) was modelled as constant and varying between sexes. Per capita recruitment rate (f) was modelled as constant and varying between sexes. The individual models were fitted within their respective full model using a custom-made AIC based model evaluation function created by Lukas Landler from BOKU (Universität für Bodenkultur Wien). The models were then ranked by their Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2004). Models with lower AICc values offer a better fit. Each selected model was then tested individually with the "predict" function in openCR to exclude potential models that yield any warning messages.

The function "openCR.fit" was used to estimate the time-specific population size (N) using the non-spatial Jolly-Seber-Schwarz-Arnason model for open populations (type "JSSAN" in openCR) (Efford 2022). Two full models were created from the capture histories that include fire-bellied toads of both age-classes, one per study site. Capture probability (p) was modelled as constant, varying between sexes, and varying through time with a non-continuous time effect. Apparent survival (φ) was modelled as constant and varying between sexes. Time-specific population size (N) was modelled as constant and varying through time with a non-continuous time effect. Model selection and testing followed the same steps as mentioned above.

To visualize the population trend in Seeschlacht throughout the study period, a linear regression was added to Fig. 22 by using the built-in function “Trendline” and selecting “Linear” in Microsoft Excel. The equation and R^2-value are displayed on the chart.

Results

Capture data

A total of 5852 capture events were registered over the whole study period, 5846 were documented with a photo, the remaining six were excluded from image comparison and analysis. Seven fire-bellied toads were captured twice on the same sampling occasion. In these cases, the second capture event was excluded from further analysis. Of the remaining 5839 capture events, 2462 (42.16 %) were adults (♂ 1148, ♀ 1314), 3017 (51.67 %) were juveniles, and 360 (6.17 %) were metamorphs (Table 4). The number of registered capture events varied between study years, study sites, and individual sampling sessions (see supplementary material Tables A1 through A8). More individuals were captured at Königshaufen than in Seeschlacht (Table 4). Nearly two thirds of all captured animals at Königshaufen were juveniles, whereas the vast majority of toads in Seeschlacht were adults. Slightly more females than males were captured in both areas. Metamorphs were found almost exclusively in the Königshaufen ponds, in Seeschlacht, metamorphs were only recorded in 2019 and 2022. Numbers of metamorphs encountered at Königshaufen often exceeded hundreds or thousands and only a small number were captured. Metamorphs will not be included in capture numbers anymore from here on.

Table 4: Overview of all capture events between 2015 and 2022 combined and separated per study year and study site. Metamorphs (Meta) are not included in the numbers of individuals and capture events.

Year	Study site	Individuals	Capture events	Recaptures	Adults	Juveniles	Males	Females	Meta
2015	Königshaufen	73	74	1	47	27	17	30	0
	Seeschlacht	71	77	6	74	3	39	35	0
2016	Königshaufen	449	467	18	146	321	74	72	9
	Seeschlacht	130	176	46	173	3	88	85	0
2017	Königshaufen	1124	1224	100	280	944	152	128	1
	Seeschlacht	107	165	58	124	41	63	61	0
2018	Königshaufen	548	668	120	345	323	173	172	50
	Seeschlacht	91	189	98	160	29	77	83	0
2019	Königshaufen	233	344	111	286	58	101	185	64
	Seeschlacht	48	113	65	101	12	39	62	15
2020	Königshaufen	85	91	6	45	46	26	19	86
	Seeschlacht	79	125	46	60	65	24	36	0
2021	Königshaufen	417	463	46	48	415	25	23	66
	Seeschlacht	59	205	146	155	50	63	92	0
2022	Königshaufen	783	887	104	229	658	114	115	67
	Seeschlacht	43	211	168	189	22	73	116	2
Total	Königshaufen	3712	4218	506	1426	2792	682	744	343
	Seeschlacht	628	1261	633	1036	225	466	570	17
	Total	**4340**	**5479**	**1139**	**2462**	**3017**	**1148**	**1314**	**360**

Recaptures

No fire-bellied toads from one study area were recaptured in the other. Most individuals were captured only once, a total of 1139 capture events (20.79 %) were identified as recaptures (Table 4). Recaptured individuals were mostly captured a total of two times, however, several animals were recaptured more frequently, up to 14 times (Table 5). At Königshaufen, no individual was captured more than seven times, in Seeschlacht, the recapture frequencies of some individuals were higher, with one toad having been caught a total of 15 times throughout the study period.

Table 5: Capture frequencies of fire-bellied toads combined and separated per study area. Metamorphs are not included.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Königshaufen	3277	374	50	8	2	0	1	0	0	0	0	0	0	0	0
Seeschlacht	383	109	47	32	20	12	9	4	4	5	1	0	1	0	1
Total	3660	483	97	40	22	12	10	4	4	5	1	0	1	0	1

Although more capture events were registered at Königshaufen, the number of recaptures was higher in Seeschlacht (Table 4). In the Königshaufen ponds, 506 out of 4218 (12.00 %) capture events were identified as recaptures, in Seeschlacht, 633 out of 1261 (50.20 %) capture events were identified as recaptures.

No individual was captured at least once during each study year. In Seeschlacht, three fire-bellied toads were registered during the first and the last of the studied years, in 2015 and 2022. Seven individuals were captured a maximum of six years apart, one of them in 2015 and 2021, the other six in 2016 and 2022. At Königshaufen, one toad was recaptured after five years, in 2017 and 2022, and another individual was captured four years apart, in 2018 and 2022.

Population statistics

Model type “JSSAfCL”

From the full models including all animals, the model with all three parameters varying between sexes and an additional non-continuous time effect for capture probability (p~sex + t; phi~sex; f~sex) was chosen to estimate the parameters of interest for both study areas, which is the model with the lowest AICc value for Seeschlacht (Table 7), and the model with the second lowest AICc value for Königshaufen (Table 6). For the sake of better comparison, the model with the same parameter variables was chosen for both study areas over the model with the lowest AICc value for Königshaufen. Models where recruitment was modelled as constant did not work for Seeschlacht because of the differences in recruitment between juveniles on the one hand, males and females on the other hand (Table 13).

Table 6: The ten best population models from model selection (“JSSAfCL”) for Königshaufen including all fire-bellied toads. All individual models were tested within the same full model. Model parameters are capture probability (p), apparent survival (phi) and per capita recruitment rate (f). All three parameters were modelled as constant (1) and varying between sexes (sex), capture probability was additionally modelled as varying through time with a non-continuous time effect (t). The remaining table entries show the number of estimated parameters (npar), the AICc value, and the difference in the AICc value between the respective model and the model with the lowest AICc value (ΔAICc).

Number	Model parameters	npar	AICc	ΔAICc
1	p~sex + t phi~sex f~1	14	35826.738	0.000
2	p~sex + t phi~sex f~sex	16	35830.134	3.396
3	p~sex + t phi~1 f~sex	14	35830.235	3.497
4	p~t phi~1 f~sex	12	35842.579	15.841
5	p~t phi~sex f~1	12	35845.971	19.233
6	p~sex + t phi~1 f~1	12	35845.988	19.250
7	p~t phi~sex f~sex	14	35846.775	20.037
8	p~t phi~1 f~1	10	35860.679	33.941
9	p~1 phi~1 f~sex	5	37602.481	1775.743
10	p~sex phi~1 f~sex	7	37603.278	1776.540

Table 7: The ten best population models from model selection (“JSSAfCL”) for Seeschlacht including all fire-bellied toads. All individual models were tested within the same full model. Model parameters are capture probability (p), apparent survival (phi) and per capita recruitment rate (f). All three parameters were modelled as constant (1) and varying between sexes (sex), capture probability was additionally modelled as varying through time with a non-continuous time effect (t). The remaining table entries show the number of estimated parameters (npar), the AICc value, and the difference in the AICc value between the respective model and the model with the lowest AICc value (ΔAICc).

Number	Model parameters	npar	AICc	ΔAICc
1	p~sex + t phi~sex f~sex	16	10302.154	0.000
2	p~t phi~sex f~sex	14	10313.874	11.720
3	p~sex + t phi~1 f~sex	14	10315.399	13.245
4	p~t phi~1 f~sex	12	10321.013	18.859
5	p~t phi~sex f~1	12	10373.649	71.495
6	p~sex + t phi~sex f~1	14	10375.326	73.172
7	p~t phi~1 f~1	10	10380.748	78.594
8	p~sex + t phi~1 f~1	12	10382.501	80.347
9	p~sex phi~sex f~sex	9	10437.223	135.069
10	p~sex phi~1 f~sex	7	10459.323	157.169

For the full models including only adult animals, the ΔAICc values of the top eight models for both study areas were very close together (ΔAICc < 6; Table 8, Table 9). To take into account model selection uncertainty, model averaging was applied to all models with ΔAICc < 6 using the “modelAverage” function in openCR.

Table 8: The ten best population models from model selection (“JSSAfCL”) for Königshaufen including only adult fire-bellied toads. All individual models were tested within the same full model. Model parameters are capture probability (p), apparent survival (phi) and per capita recruitment rate (f). All three parameters were modelled as constant (1) and varying between sexes (sex), capture probability was additionally modelled as varying through time with a non-continuous time effect (t). The remaining table entries show the number of estimated parameters (npar), the AICc value, and the difference in the AICc value between the respective model and the model with the lowest AICc value (ΔAICc). AICcwt shows the weight of each model for model averaging.

Number	Model parameters	npar	AICc	ΔAICc	AICcwt
1	p~sex + t phi~1 f~1	11	12156.933	0.000	0.3166
2	p~t phi~1 f~1	10	12157.539	0.606	0.2338
3	p~sex + t phi~1 f~sex	12	12159.065	2.132	0.1090
4	p~sex + t phi~sex f~1	12	12159.135	2.202	0.1053
5	p~t phi~sex f~1	11	12159.459	2.526	0.0895
6	p~t phi~1 f~sex	11	12159.712	2.779	0.0789
7	p~sex + t phi~sex f~sex	13	12161.351	4.418	0.0348
8	p~t phi~sex f~sex	12	12161.505	4.572	0.0322
9	p~1 phi~1 f~1	3	12631.741	474.808	0.0000
10	p~sex phi~1 f~sex	5	12633.068	476.135	0.0000

Table 9: The ten best population models from model selection ("JSSAfCL") for Seeschlacht including only adult fire-bellied toads. All individual models were tested within the same full model. Model parameters are capture probability (p), apparent survival (phi) and per capita recruitment rate (f). All three parameters were modelled as constant (1) and varying between sexes (sex), capture probability was additionally modelled as varying through time with a non-continuous time effect (t). The remaining table entries show the number of estimated parameters (npar), the AICc value, and the difference in the AICc value between the respective model and the model with the lowest AICc value (ΔAICc). AICcwt shows the weight of each model for model averaging.

Number	Model parameters	npar	AICc	ΔAICc	AICcwt
1	p~sex + t phi~1 f~sex	12	8542.519	0.000	0.3773
2	p~sex + t phi~sex f~sex	13	8543.136	0.617	0.2771
3	p~sex + t phi~1 f~1	11	8544.699	2.180	0.1268
4	p~t phi~1 f~1	10	8546.162	3.643	0.0610
5	p~t phi~1 f~sex	11	8546.222	3.703	0.0592
6	p~sex + t phi~sex f~1	12	8546.539	4.020	0.0505
7	p~t phi~sex f~sex	12	8548.005	5.486	0.0243
8	p~t phi~sex f~1	11	8548.057	5.538	0.0237
9	p~sex phi~sex f~sex	6	8662.312	119.793	0.0000
10	p~sex phi~1 f~sex	5	8662.837	120.318	0.0000

Capture probability ("JSSAfCL")

Capture probabilities of fire-bellied toads from the model type "JSSAfCL" (for estimations of apparent survival and per capita recruitment) varied across the years, between age-classes, male and female individuals, and the two study areas (Table 10, Table 11). Within each year, estimates for capture probability were higher for all studied groups in Seeschlacht than for those at Königshaufen.

Table 10: Estimates for capture probability of fire-bellied toads from model selection ("JSSAfCL") at Königshaufen. Estimates for females (pF), males (pM), and juveniles (pJ) are separated per study year.

Königshaufen	**2015**	LCI	UCI	**2016**	LCI	UCI	**2017**	LCI	UCI	**2018**	LCI	UCI
pF	**0.0028**	0.0020	0.0041	**0.0153**	0.0117	0.0200	**0.0488**	0.0383	0.0619	**0.0258**	0.0204	0.0326
pM	**0.0018**	0.0012	0.0027	**0.0098**	0.0072	0.0133	**0.0317**	0.0238	0.0420	**0.0166**	0.0126	0.0220
pJ	**0.0015**	0.0011	0.0020	**0.0080**	0.0067	0.0097	**0.0261**	0.0225	0.0302	**0.0137**	0.0118	0.0159
continued	**2019**	LCI	UCI	**2020**	LCI	UCI	**2021**	LCI	UCI	**2022**	LCI	UCI
pF	**0.0119**	0.0094	0.0152	**0.0048**	0.0035	0.0065	**0.0214**	0.0165	0.0276	**0.0363**	0.0281	0.0468
pM	**0.0077**	0.0057	0.0102	**0.0031**	0.0022	0.0043	**0.0138**	0.0102	0.0186	**0.0235**	0.0173	0.0318
pJ	**0.0063**	0.0053	0.0074	**0.0025**	0.0020	0.0032	**0.0113**	0.0095	0.0134	**0.0193**	0.0162	0.0230

Table 11: Estimates for capture probability of fire-bellied toads from model selection ("JSSAfCL") in Seeschlacht. Estimates for females (pF), males (pM), and juveniles (pJ) are separated per study year.

Seeschlacht	**2015**	LCI	UCI	**2016**	LCI	UCI	**2017**	LCI	UCI	**2018**	LCI	UCI
pF	**0.0232**	0.0170	0.0316	**0.0502**	0.0398	0.0633	**0.0626**	0.0505	0.0773	**0.0673**	0.0554	0.0816
pM	**0.0180**	0.0131	0.0247	**0.0391**	0.0307	0.0498	**0.0489**	0.0389	0.0613	**0.0527**	0.0424	0.0652
pJ	**0.0292**	0.0207	0.0412	**0.0628**	0.0476	0.0823	**0.0779**	0.0611	0.0989	**0.0837**	0.0667	0.1046
continued	**2019**	LCI	UCI	**2020**	LCI	UCI	**2021**	LCI	UCI	**2022**	LCI	UCI
pF	**0.0375**	0.0297	0.0472	**0.0783**	0.0623	0.0980	**0.1192**	0.0983	0.1438	**0.1155**	0.0957	0.1387
pM	**0.0291**	0.0226	0.0374	**0.0614**	0.0478	0.0786	**0.0944**	0.0757	0.1170	**0.0914**	0.0740	0.1123
pJ	**0.0470**	0.0361	0.0609	**0.0971**	0.0782	0.1199	**0.1462**	0.1214	0.1752	**0.1419**	0.1174	0.1704

At Königshaufen, capture probabilities during each year were higher for female fire-bellied toads than for male ones, and lowest for juvenile individuals (Fig. 13). Across the years, capture probability was highest for all groups in 2017, then decreased from year to year until 2020, and increased again between 2020 and 2022.

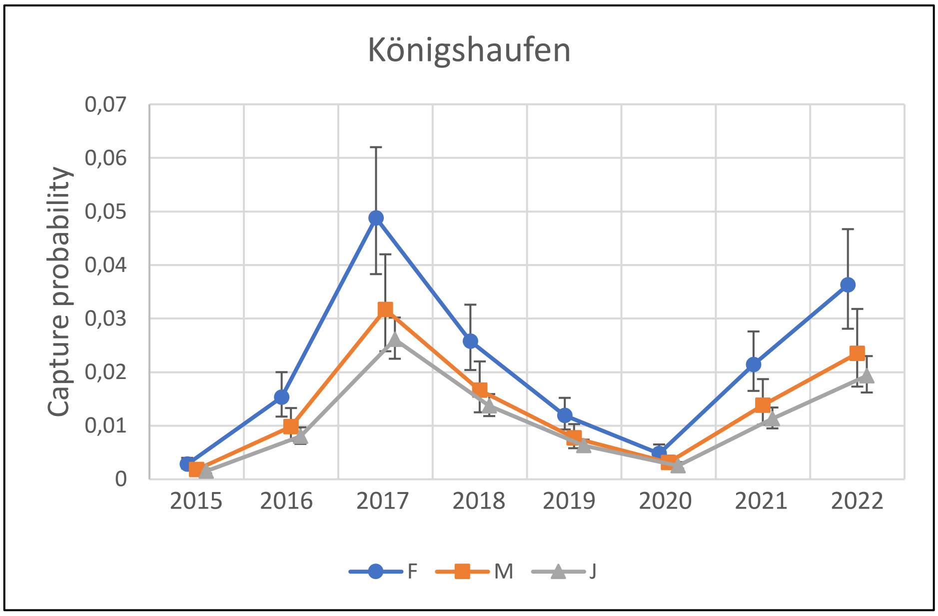

Fig. 13: Capture probability from model selection ("JSSAfCL") for female (F), male (M), and juvenile (J) fire-bellied toads at Königshaufen, separated per study year. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R.

In Seeschlacht, annual capture probabilities were highest for juvenile fire-bellied toads, and lowest for male individuals, with females lying in between (Fig. 14). Capture probability increased for all groups from 2015 to 2018, dropped in 2019, and increased again during the following two years, reaching its highest value in 2021. Between 2021 and 2022, capture probabilities slightly decreased again.

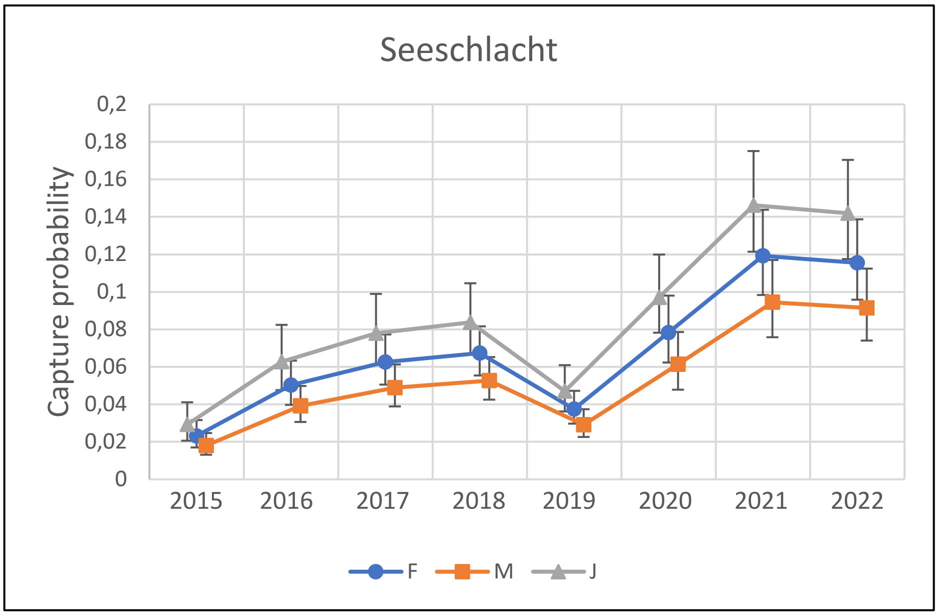

Fig. 14: Capture probability from model selection ("JSSAfCL") for female (F), male (M), and juvenile (J) fire-bellied toads in Seeschlacht, separated per study year. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R.

Apparent survival

At Königshaufen, estimates for apparent survival including all age-classes were lowest for female fire-bellied toads and highest for juvenile ones, with males lying in between (Table 12). For Seeschlacht, apparent survival was higher for males than for females, and lowest for juveniles.

Between the study areas, apparent survival was higher for all groups in Seeschlacht than at Königshaufen: more than twice as high for female fire-bellied toads, nearly twice as high for males, and slightly higher for juvenile ones (Fig. 15).

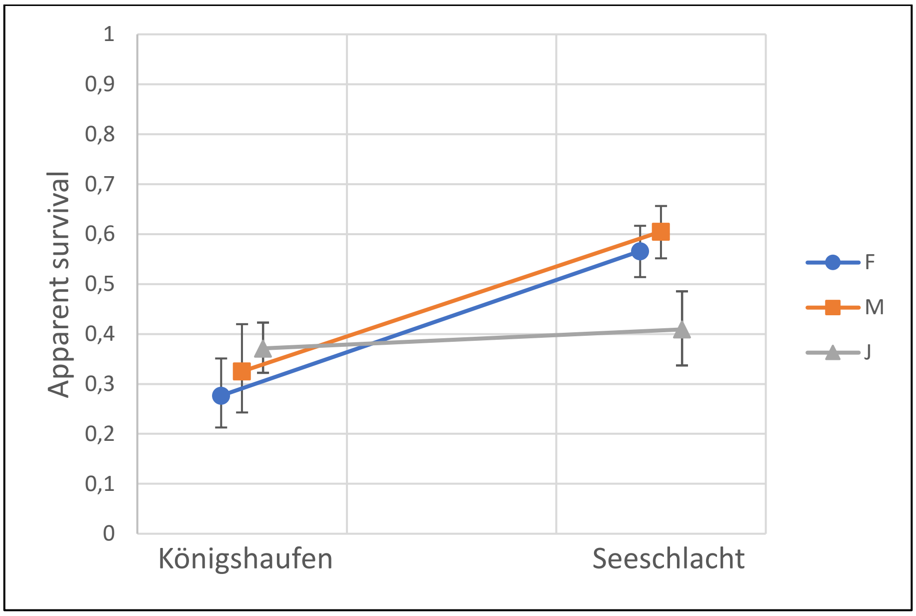

Fig. 15: Annual apparent survival of female (F), male (M), and juvenile (J) fire-bellied toads from model selection ("JSSAfCL") including all fire-bellied toads, separated per study area. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R.

Model-averaged estimates for apparent survival at Königshaufen including only adult fire-bellied toads were nearly even between male and female animals (Table 12). For Seeschlacht, model averaging resulted in a slightly higher estimate of apparent survival for male individuals than for female ones. Between the two study areas, apparent survival was higher for both male and female fire-bellied toads in Seeschlacht than at Königshaufen (Fig. 16).

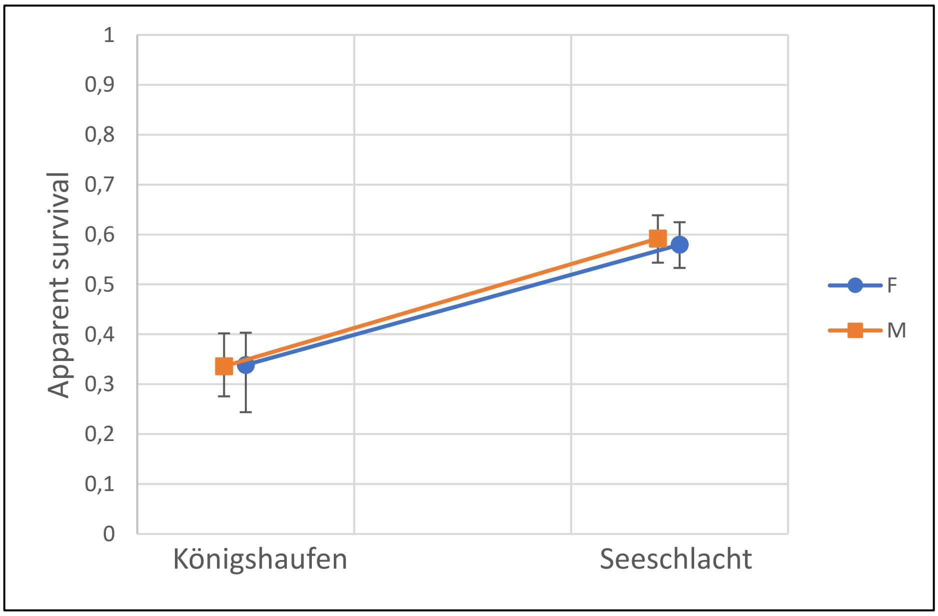

Fig. 16: Annual apparent survival of female (F) and male (M) fire-bellied toads from model averaging ("JSSAfCL") including only adult fire-bellied toads, separated per study area. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R.

Table 12: Estimates for annual apparent survival from model selection (including all fire-bellied toads), and model averaging (including only adult fire-bellied toads) ("JSSAfCL"). Estimates for females (φF), males (φM), and juveniles (φJ) are separated per study area.

Model	***φF***	LCI	UCI	***φM***	LCI	UCI	***φJ***	LCI	UCI
Königshaufen all	**0.2766**	0.2128	0.3510	**0.3251**	0.2429	0.4196	**0.3711**	0.3222	0.4228
Seeschlacht all	**0.5660**	0.5139	0.6166	**0.6051**	0.5515	0.6563	**0.4091**	0.3370	0.4854
Königshaufen adult	**0.3387**	0.2797	0.4032	**0.3359**	0.2757	0.4020	-	-	-
Seeschlacht adult	**0.5796**	0.5331	0.6247	**0.5919**	0.5435	0.6385	-	-	-

Per capita recruitment

At Königshaufen, estimates for per capita recruitment including all age-classes were highest for female fire-bellied toads and lowest for males, with juveniles lying in between (Table 13). For Seeschlacht, the differences between the three groups were greater: per capita recruitment was by far the highest for juvenile individuals, and higher for female than for male ones.

Between the two study sites, per capita recruitment was higher for both male and female fire-bellied toads at Königshaufen than in Seeschlacht, but slightly lower for juvenile individuals (Fig. 17).

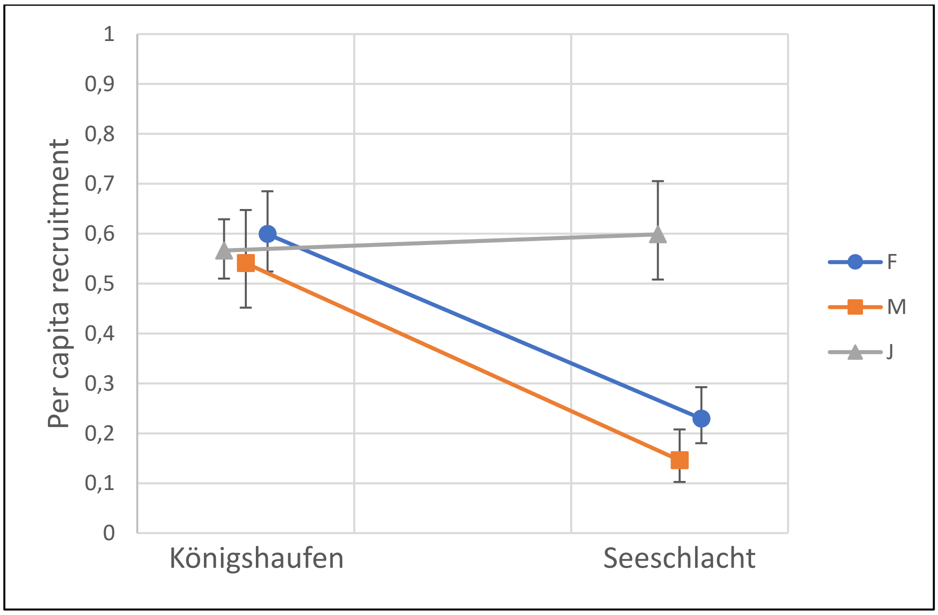

Fig. 17: Annual per capita recruitment of female (F), male (M), and juvenile (J) fire-bellied toads from model selection ("JSSAfCL") including all fire-bellied toads, separated per study area. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R.

From the models including only adult fire-bellied toads, model-averaged estimates for per capita recruitment were nearly even between male and female individuals at Königshaufen (Table 13). For Seeschlacht, model averaging resulted in a slightly higher per capita recruitment estimate for female toads than for male ones.

Between the two study sites, per capita recruitment was more than twice as high for both male and female toads at Königshaufen than in Seeschlacht (Fig. 18).

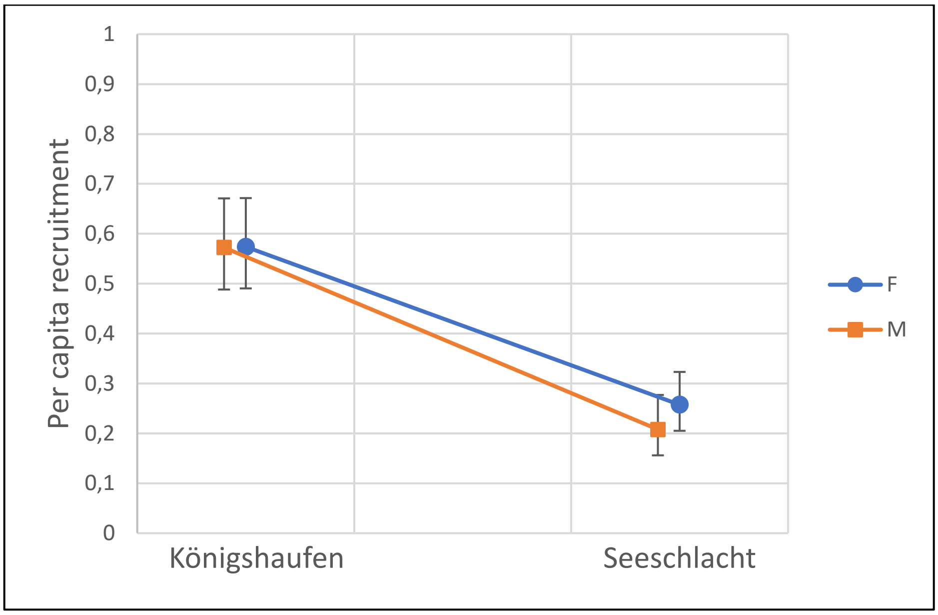

Fig. 18: Annual per capita recruitment of female (F) and male (M) fire-bellied toads from model averaging ("JSSAfCL") including only adult fire-bellied toads, separated per study area. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R.

Table 13: Estimates for annual per capita recruitment from model selection (including all fire-bellied toads), and model averaging (including only adult fire-bellied toads) ("JSSAfCL"). Estimates for females (fF), males (fM), and juveniles (fJ) are separated per study area.

Model	**fF**	LCI	UCI	**fM**	LCI	UCI	**fJ**	LCI	UCI
Königshaufen all	**0.5993**	0.5242	0.6851	**0.5409**	0.4518	0.6475	**0.5664**	0.5100	0.6289
Seeschlacht all	**0.2296**	0.1802	0.2925	**0.1460**	0.1025	0.2078	**0.5987**	0.5081	0.7053
Königshaufen adult	**0.5739**	0.4905	0.6715	**0.5724**	0.4883	0.6710	-	-	-
Seeschlacht adult	**0.2575**	0.2052	0.3232	**0.2079**	0.1560	0.2771	-	-	-

Model type “JSSAN”

The ΔAICc values of the top three models for Königshaufen, and of the top two models for Seeschlacht were relatively close together (ΔAICc < 10; Table 14, Table 15), therefore model averaging was applied to all models with ΔAICc < 10 using the “modelAverage” function in openCR.

Table 14: The ten best population models from model selection (“JSSAN”) for Königshaufen including all fire-bellied toads. All individual models were tested within the same full model. Model parameters are capture probability (p), apparent survival (phi) and time-specific population size (N). All three parameters were modelled as constant (1), capture probability and apparent survival were also modelled as varying between sexes (sex). A non-continuous time effect (t) was added for capture probability and time-specific population size. The remaining table entries show the number of estimated parameters (npar), the AICc value, and the difference in the AICc value between the respective model and the model with the lowest AICc value (ΔAICc). AICcwt shows the weight of each model for model averaging.

Number	Model parameters	npar	AICc	ΔAICc	AICcwt
1	p~sex + t phi~1 N~t	19	35683.39	0.000	0.6891
2	p~sex + t phi~sex N~t	21	35685.09	1.703	0.2941
3	p~t phi~sex N~t	19	35690.81	7.421	0.0169
4	p~t phi~1 N~t	17	35699.99	16.598	0.0000
5	p~1 phi~sex N~t	12	35736.38	52.987	0.0000
6	p~sex phi~sex N~t	14	35738.19	54.803	0.0000
7	p~sex phi~1 N~t	12	35740.46	57.067	0.0000
8	p~1 phi~1 N~t	10	35740.78	57.388	0.0000
9	p~sex + t phi~1 N~1	12	35877.63	194.240	0.0000
10	p~sex + t phi~sex N~1	14	35877.92	194.529	0.0000

Table 15: The ten best population models from model selection (“JSSAN”) for Seeschlacht including all fire-bellied toads. All individual models were tested within the same full model. Model parameters are capture probability (p), apparent survival (phi) and time-specific population size (N). All three parameters were modelled as constant (1), capture probability and apparent survival were also modelled as varying between sexes (sex). A non-continuous time effect (t) was added for capture probability and time-specific population size. The remaining table entries show the number of estimated parameters (npar), the AICc value, and the difference in the AICc value between the respective model and the model with the lowest AICc value (ΔAICc). AICcwt shows the weight of each model for model averaging.

Number	Model parameters	npar	AICc	ΔAICc	AICcwt
1	p~sex + t phi~sex N~t	21	10348.84	0.000	0.9838
2	p~t phi~sex N~t	19	10357.04	8.209	0.0162
3	p~t phi~1 N~t	17	10379.36	30.521	0.0000
4	p~sex + t phi~1 N~t	19	10379.71	30.879	0.0000
5	p~sex phi~sex N~t	14	10432.55	83.710	0.0000
6	p~sex + t phi~sex N~1	14	10459.70	110.863	0.0000
7	p~sex phi~1 N~t	12	10464.92	116.083	0.0000
8	p~1 phi~sex N~t	12	10466.99	118.150	0.0000
9	p~t phi~sex N~1	12	10475.68	126.849	0.0000
10	p~1 phi~1 N~t	10	10481.08	132.240	0.0000

Capture probability ("JSSAN")

Capture probabilities of fire-bellied toads from the model type "JSSAN" (for estimations of population size) varied across the years, between age-classes, male and female individuals, and the two study areas (Table 16, Table 17). Within each year, estimates for capture probability were higher for all studied groups in Seeschlacht than at Königshaufen, only 2019 had slightly higher capture probabilities of juveniles at Königshaufen than in Seeschlacht.

Table 16: Estimates for capture probability of fire-bellied toads from model averaging ("JSSAN") at Königshaufen. Estimates for females (pF), males (pM), and juveniles (pJ) are separated per study year.

Königshaufen	**2015**	LCI	UCI	**2016**	LCI	UCI	**2017**	LCI	UCI	**2018**	LCI	UCI
pF	**0.0051**	0.0043	0.0294	**0.0064**	0.0027	0.0047	**0.0126**	0.0041	0.006	**0.0181**	0.0048	0.0066
pM	**0.0045**	0.0038	0.0264	**0.0057**	0.0024	0.0041	**0.0111**	0.0036	0.0052	**0.0159**	0.0043	0.0058
pJ	**0.0082**	0.0071	0.0487	**0.0105**	0.0039	0.0062	**0.0204**	0.0037	0.0044	**0.0292**	0.0063	0.0079
continued	**2019**	LCI	UCI	**2020**	LCI	UCI	**2021**	LCI	UCI	**2022**	LCI	UCI
pF	**0.0311**	0.0072	0.0093	**0.0045**	0.0026	0.006	**0.0115**	0.0042	0.0067	**0.0114**	0.0036	0.0053
pM	**0.0275**	0.0073	0.0099	**0.0040**	0.0023	0.0053	**0.0101**	0.0037	0.0059	**0.0101**	0.0032	0.0046
pJ	**0.0498**	0.0151	0.0211	**0.0074**	0.0042	0.0098	**0.0186**	0.0047	0.0062	**0.0186**	0.0034	0.0041

Table 17: Estimates for capture probability of fire-bellied toads from model averaging ("JSSAN") in Seeschlacht. Estimates for females (pF), males (pM), and juveniles (pJ) are separated per study year.

Seeschlacht	**2015**	LCI	UCI	**2016**	LCI	UCI	**2017**	LCI	UCI	**2018**	LCI	UCI
pF	**0.0395**	0.0214	0.0447	**0.0620**	0.0161	0.0213	**0.0562**	0.0136	0.0176	**0.0657**	0.013	0.016
pM	**0.0316**	0.0171	0.0359	**0.0500**	0.013	0.0173	**0.0452**	0.0113	0.0148	**0.0529**	0.0115	0.0144
pJ	**0.0487**	0.0271	0.0574	**0.0761**	0.0237	0.0331	**0.0690**	0.0182	0.0242	**0.0804**	0.0186	0.0236
continued	**2019**	LCI	UCI	**2020**	LCI	UCI	**2021**	LCI	UCI	**2022**	LCI	UCI
pF	**0.0379**	0.009	0.0117	**0.0552**	0.0154	0.0208	**0.1232**	0.0221	0.0261	**0.1158**	0.0198	0.0233
pM	**0.0304**	0.0077	0.0102	**0.0444**	0.0132	0.0184	**0.1005**	0.0209	0.0257	**0.0943**	0.0185	0.0225
pJ	**0.0467**	0.0128	0.0173	**0.0678**	0.0176	0.0232	**0.1489**	0.0262	0.0306	**0.1402**	0.0248	0.0291

At Königshaufen, capture probabilities of male and female fire-bellied toads were relatively similar and lower than those of juvenile individuals during each year (Fig. 19). Across the years, capture probability was highest for all groups in 2019 and lowest in 2020.

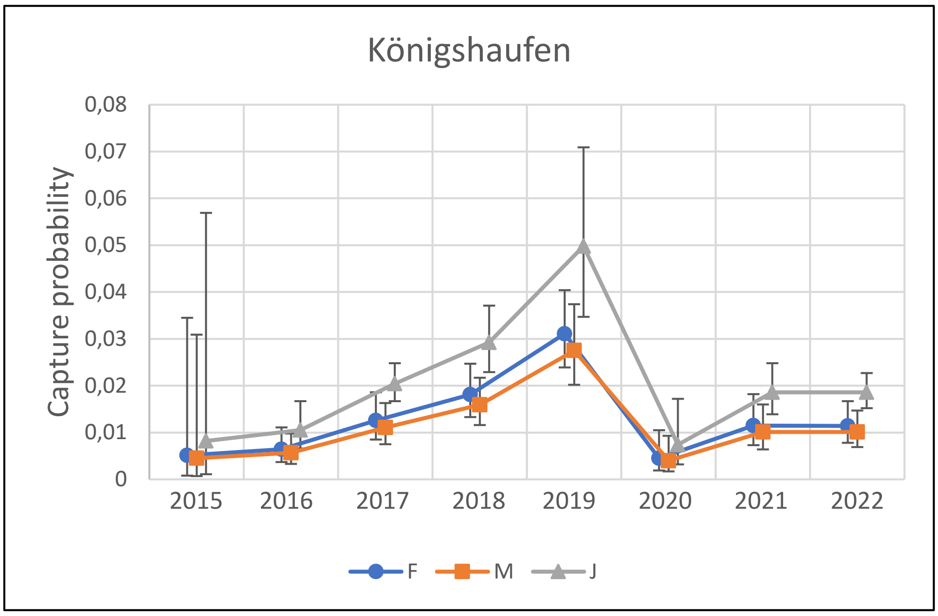

Fig. 19: Capture probability from model averaging ("JSSAN") for female (F), male (M), and juvenile (J) fire-bellied toads at Königshaufen, separated per study year. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R.

In Seeschlacht, annual capture probabilities were highest for juvenile fire-bellied toads, and lowest for male individuals, with females lying in between (Fig. 20). Capture probabilities were highest for all groups in 2021 and lowest in 2019.

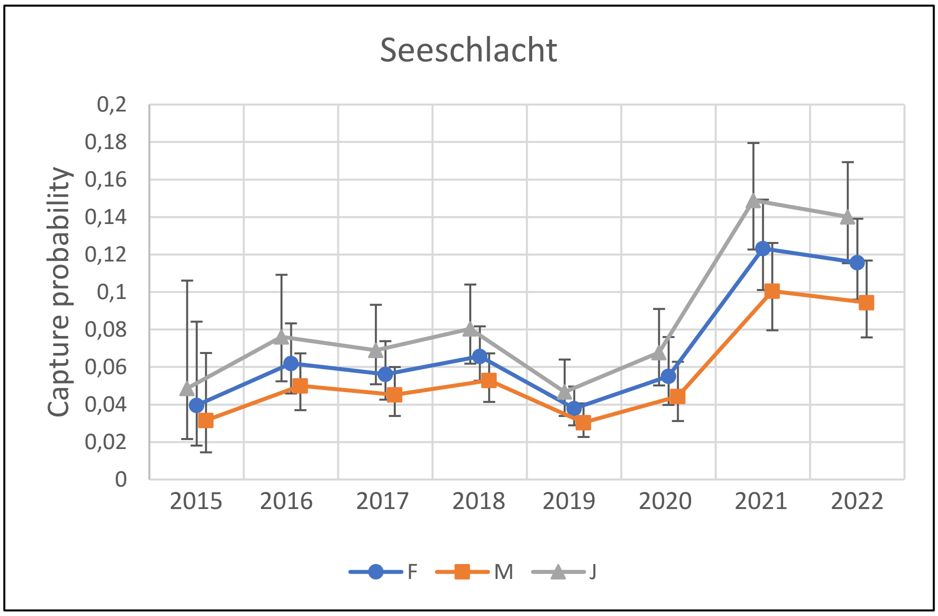

Fig. 20: Capture probability from model averaging ("JSSAN") for female (F), male (M), and juvenile (J) fire-bellied toads in Seeschlacht, separated per study year. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R.

Population size

Model-averaged estimates for time-specific population size were considerably higher at Königshaufen than in Seeschlacht during all studied years (Table 18). At Königshaufen, population size varied greatly between the years (Fig. 21). At the beginning of the study period, it increased from year to year and reached its maximum in 2017, then declined again until 2019. Between 2019 and 2022 the population size started growing again.

In Seeschlacht, the population size also fluctuated between the studied years, but not as much as at Königshaufen (Fig. 22). It increased during the first three study years and reached its highest point in 2017. Apart from one last increase between 2019 and 2020, the population size then continuously decreased and reached its minimum in 2022.

Table 18: Model averaged estimates ("JSSAN") for time-specific population size (N), separated per study area and study year. Numbers were rounded to the nearest integer.

Year	Königshaufen N	LCI	UCI	Seeschlacht N	LCI	UCI
2015	**1550**	228	10534	**353**	169	736
2016	**5931**	3753	9373	**390**	297	510
2017	**8974**	7143	11275	**441**	347	560
2018	**3137**	2610	3771	**331**	273	402
2019	**822**	665	1017	**263**	210	329
2020	**1868**	852	4095	**334**	254	437
2021	**2938**	2145	4024	**172**	144	205
2022	**4726**	3801	5876	**143**	119	171

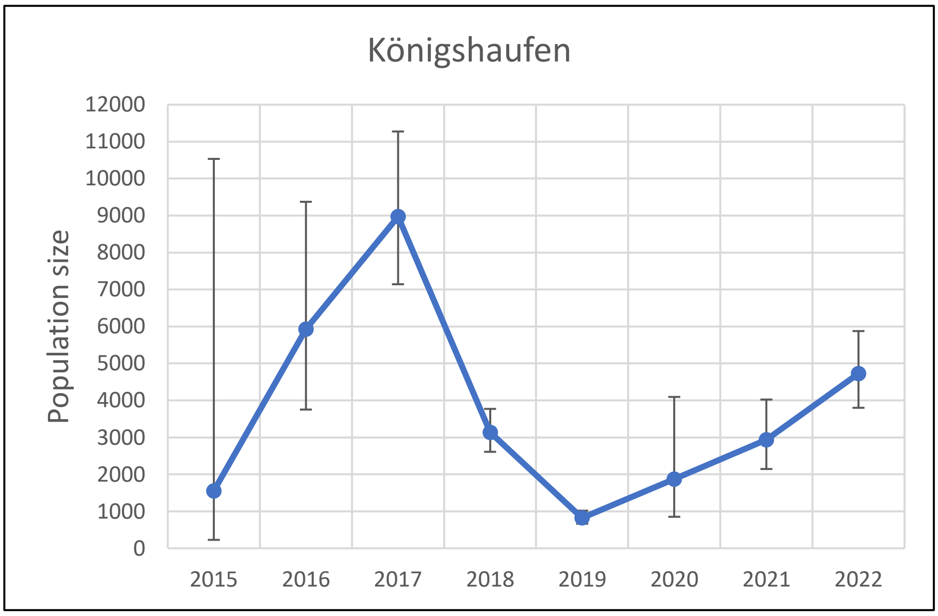

Fig. 21: Model averaged population size ("JSSAN") per study year at Königshaufen. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R. Numbers were rounded to the nearest integer.

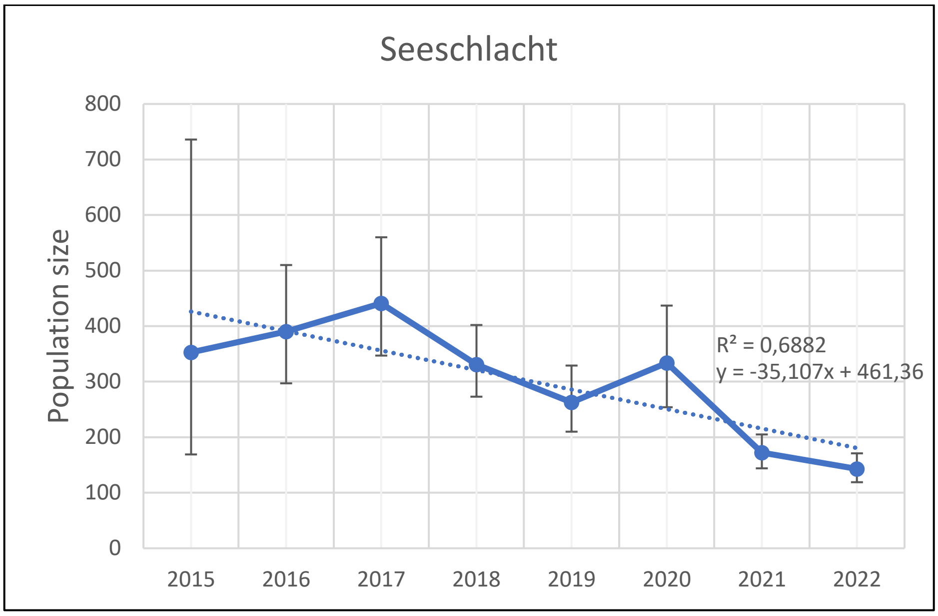

Fig. 22: Model averaged population size ("JSSAN") per study year at Seeschlacht. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R. Numbers were rounded to the nearest integer. To visualize the population trend throughout the study period, a linear regression (dotted line) is included in the chart.

Discussion

Given the consistent differences in population structure between Seeschlacht and Königshaufen throughout the study period, the differences in apparent survival and per capita recruitment between the two populations of fire-bellied toads showed the expected results. Apparent survival was higher in the more stable Seeschlacht area, recruitment was higher in the more dynamic Königshaufen ponds. The estimated population size was higher and showed larger fluctuations at Königshaufen.

Within each study area, apparent survival was slightly higher for male toads than for females, while the opposite was true for per capita recruitment. These differences are most likely a methodical artefact from sex classification. On average, males were identified as adults earlier than females and they therefore remained in the adult stage longer, resulting in higher apparent survival and lower recruitment estimates.

It is also not entirely clear whether the fire-bellied toad in Lobau should be regarded as a single population or as several independent subpopulations. Genetical analyses or the study of home range sizes of adults and dispersal distances of juveniles have yet to be conducted (Philippi and Gollmann 2014). The central fuel depot serves as a physical barrier between the two populations and capture-recapture analysis showed that no individuals from one area were recaptured in the other throughout the study period. Since metamorphs were not included, movement between Königshaufen and

Seeschlacht cannot be completely ruled out. The two populations may also be in exchange with other *B. bombina* populations in Lobau via source-sink dynamics. The Königshaufen ponds could act as a highly productive source habitat (Czurda et al. 2023).

Capture probability

When conducting studies on the dynamics of animal populations, capture probability is an important parameter to consider. It can be influenced by several factors such as size, sexual differences, behavioural responses, sampling effort (Guimarães et al. 2014), or environmental conditions (Muncy et al. 2014). Population studies that do not account for detectability may lead to biased evaluations and capture probability should therefore be included (Kellner and Swihart 2014, Schmidt 2004).

Capture probabilities were relatively similar for all groups between the two model types ("JSSAfCL" and "JSSAN") in Seeschlacht (Fig. 14, Fig. 20). At Königshaufen, capture probabilities were highest in 2017 for model type "JSSAfCL", and highest in 2019 for model type "JSSAN" (Fig. 13, Fig. 19). These variations may be a result of individual capture heterogeneity of fire-bellied toads (personal communication Lukas Landler 29.03.2023). The high similarity in capture probabilities between the two models for Seeschlacht, and the higher capture probabilities in Seeschlacht than at Königshaufen may indicate higher accuracy of population parameter estimations for Seeschlacht, and estimates for Königshaufen should be interpreted more carefully.

The lower capture probabilities at Königshaufen could be a result of the more unpredictable environment. Monthly mean groundwater levels fluctuated between 0.79 m in 2022 and 1.84 m in 2016, while fluctuations in Seeschlacht ranged from 0.36 m in 2015 to 0.49 m in 2022 (Fig. 7). High water levels at Königshaufen make it harder or impossible to sample deeper parts of the ponds. Increased flight distance and mobility of fire-bellied toads in free water bodies may additionally reduce capture probabilities (Gollmann et al. 2013). When water levels are low or the ponds have completely dried out, toads may not be detected because they have been hiding in places with moist microclimates until the dry phase was over.

The differences in capture probabilities across the years within each study area can be explained by a combination of multiple factors. Firstly, sampling effort varied greatly from year to year. The number of field trips ranged from 7 in 2015 to 14 in 2022. Because of COVID-19 restrictions, the number of total field trips was also lower in 2020 (8) than in previous years (12 in 2019 and 10 in 2018). Additionally, sampling in 2020 only started in June. April and May usually are months where high numbers of toads have been captured. In 2021, the number of field trips went back up to 12 with some

COVID-19 related restrictions during April, in 2022 a total of 14 field trips took place without any further restrictions. Secondly, the number of students participating in the field course also varied from year to year (between two and five). Thirdly, varying environmental conditions can influence capture probability (as discussed above).

The differences between male and female individuals could be explained by behavioural differences. Philippi (2013) found that male toads were easier to spot during the first half of the season because of their calls and often clearly visible calling locations. It seemed however that they may have compensated for their higher conspicuousness by increasing their flight distances. Juveniles and inactive females were mainly found in shallower areas at the edges of the water which made capturing them easier once they were noticed.

While the models used in this study accounted for varying capture probabilities between sexes and across the years, other factors may still lead to biased estimates, as seen with capture heterogeneity of individual toads. Another potential cause for bias is temporary emigration. The models used in this study cannot distinguish temporary emigrants from animals that were present, but not detected. In the case of temporary emigration, the general assumption of all individuals having the same capture probability (Amstrup et al. 2005) is violated, as emigrants have a capture probability of $p = 0$, while the remaining animals that are alive and present in the study area have a capture probability of $p > 0$, which can lead to the under- or overestimation of capture probabilities and subsequent parameters such as survival (Fujiwara and Caswell 2002) or population size (Boys et al. 2019). Temporary emigration in amphibians can be the result of factors such as reproductive skipping, where individuals do not breed every year and thus may not be present at the breeding site (Muths et al. 2006, Schmidt et al. 2002), or individuals with home ranges larger than the study area (Schmidt et al. 2007). The extent of bias from temporary emigration in this study is not known. As mentioned above, not much information about the movement of *B. bombina* in Lobau is available. If reproductive skipping occurs, its effect on capture probability should be low, as spawning grounds often also serve as summer habitat for fire-bellied toads (Schneeweiss 1996). Home ranges extending beyond the study area could however have a bigger impact. Capture-recapture analysis showed that toads moved between individual water bodies in Seeschlacht, and between the two ponds at Königshaufen, and temporary emigration to other ponds outside of the study area is not unlikely. Studying the movement patterns of fire-bellied toads in Seeschlacht could provide valuable insights on their migratory behaviour and home range sizes. To improve the precision of estimated parameters, multistate models that differentiate between “unobservable” and “observable” states could be applied (Lebreton et al. 2009, Schaub et al. 2004).

Population size

Fluctuations of amphibian populations can occur completely naturally and are often caused by factors such as droughts, extreme temperatures, or predation (Collins and Storfer 2003). In Seeschlacht, the mostly constant water levels and the high proportion of adult fire-bellied toads led to a relatively stable population throughout the study period. The large shifts in population size across the years at Königshaufen can be attributed to the fact that the number of "yearlings", toads that had hatched during the last year (Philippi 2013) is predominant, therefore fluctuations are largely dependent on reproductive success from the previous year.

Population size at Königshaufen may be positively correlated with peak groundwater levels from the year before (Fig. 23). Both parameters showed a similar trend throughout the study period, just offset by a year (Fig. 24). Only the population size of 2020 did not reflect the high groundwater levels of 2019, which may be explained by the low groundwater levels in April and May of 2020 (Fig. 7). Spearman's rank correlation coefficient (r_s = 0.69, p = 0.06939; calculated with the "cor.test" function in R) shows that while there is a correlation between the two parameters, it is not significant, most likely because of the low sample size (n = 8). According to the low groundwater levels in 2022 (Fig. 7, Fig. 24) it would be expected that the population size decreases again in 2023 if the trend continues.

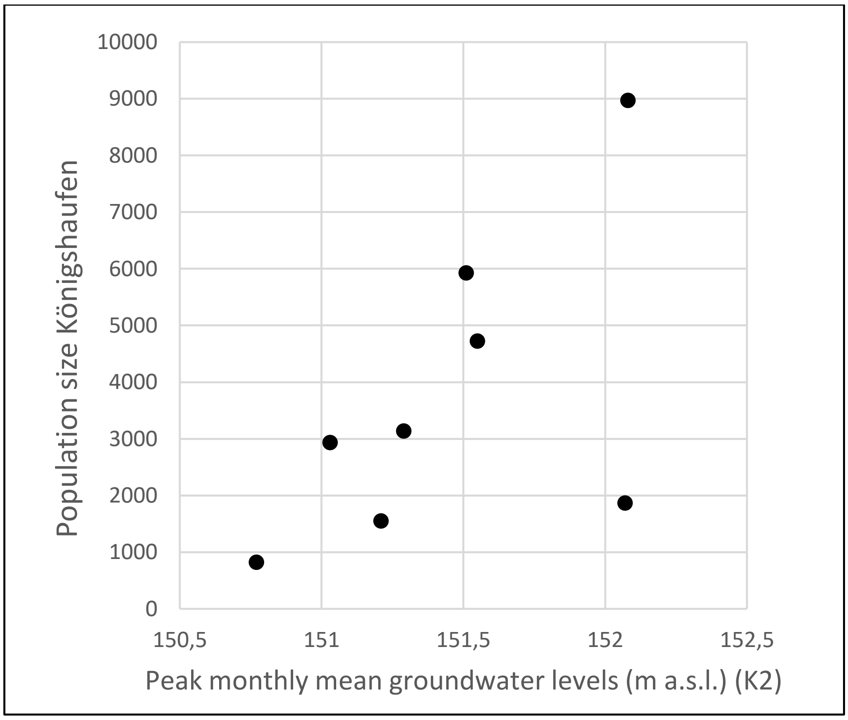

Fig. 23: Correlation between estimated population size and peak monthly mean groundwater level of the previous year (from monitoring site K2) at Königshaufen throughout the study period.

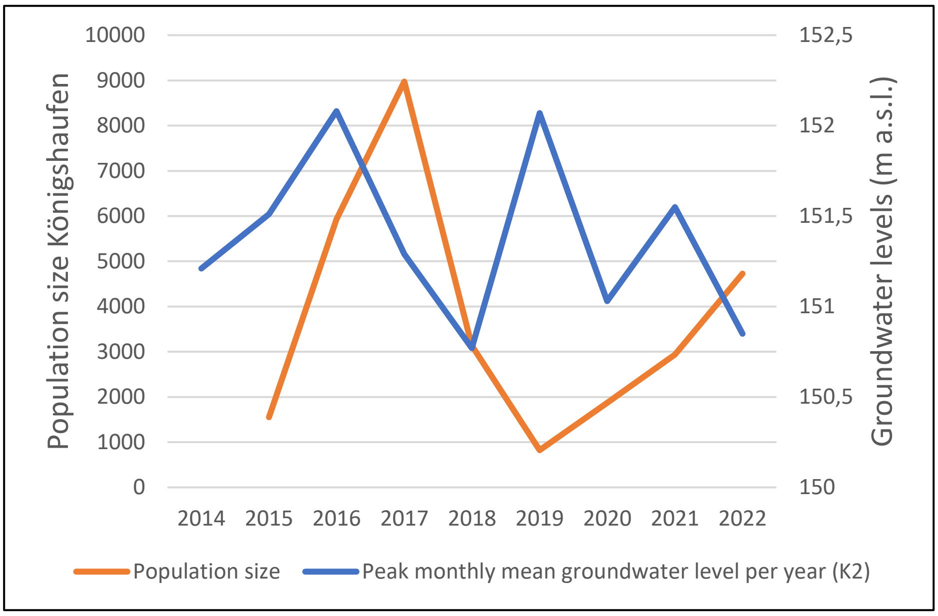

Fig. 24: Comparison of estimated population size and peak monthly mean groundwater level of the previous year (from monitoring site K2) at Königshaufen throughout the study period.

Population size estimates for 2008 (Philippi and Gollmann 2014; see introduction) and 2015 show that both populations have grown during that time frame. In 2019, the Königshaufen population has witnessed a large drop which suggests that reproductive success was low in 2018. Groundwater levels were generally low in 2018 (Fig. 7) and both ponds fell completely dry in August, which may have negatively affected metamorph survival. Reproduction was successful again during the last years of this study (Table 4).

In Seeschlacht, the population size has shown a downwards trend starting from 2017. The development from wetland vegetation towards reeds and terrestrial vegetation most likely decreases the habitat suitability for *B. bombina*. Fire-bellied toads are long-lived animals, their population development may follow the increasingly unsuitable environmental conditions with a strong delay (personal communication Christian Baumgartner 18.04.2023). In addition to the unfavourable environmental conditions for successful reproduction (discussion below), other factors such as emigration or higher tadpole predation may have also played a role in the population's decline over the past five years of this study.

Schedl (2005) proposed indicators to assess the status of *B. bombina* populations in the context of the Habitats Directive. At Königshaufen, the favourable status A (> 500 adult individuals) for population size has likely been reached in 2022. The favourable status for population structure and reproduction (all age-classes and regular reproductive success) has also been achieved. In Seeschlacht, the population size for 2022 was estimated at 143 individuals (Table 18, Fig. 22). Since the population consists of mostly adult individuals, it is not entirely clear whether the status B (100 – 500 adult individuals), or C (< 100 adult individuals) applies. For the indicator population structure and reproduction, the unfavourable status C (predominately adult individuals and inconsistent reproductive success) has to be assigned. However, Seeschlacht is well connected with other habitats of fire-bellied toads (Philippi and Gollmann 2014) and these assessments may not show the whole picture and should therefore be interpreted with care.

To further improve the hydrological situation of Obere Lobau, construction work for a second water enhancement scheme has begun in January 2023. Water will be channelled from Neue Donau into Panozzalacke and from there via already existing channels to other water bodies. Once the project will have finished in November 2023, a maximum of 1.5 $m^3 s^{-1}$ will be supplied to Obere Lobau during the months March to October (Stadt Wien n.d.). It remains to be seen if and how this will affect the population in Seeschlacht. While it will help improve the hydrological situation and might create new or enhance existing breeding sites, there is also the risk of introducing fish into currently fish-free water bodies, which has been shown to have severe negative effects on the survival of amphibians (Pope 2008, Schmidt et al. 2021).

The population size of Königshaufen and Seeschlacht for the years 2015 to 2022 was also estimated with the Chapman modification of the Lincoln-Petersen index (Table 19) (Czurda et al. 2023). The trends in population size within each study area are similar between the two methods but estimates from the Chapman method were considerably lower than from model averaging in this study (Fig. 25, Fig. 26). The Chapman method calculates population size from data of only two capture occasions and assumes equal capture probability for all animals on each occasion (Amstrup et al. 2005). The model used in this study calculates population size from individual capture histories and considers varying capture probabilities across the years and between sexes (p~sex + t), and therefore provides more accurate estimates.

Table 19: Population size estimates and standard deviation (SD) per year and study area calculated with the Chapman modification of the Lincoln-Petersen index in Czurda et al. (2023). Numbers were rounded to the nearest integer.

Year	**Königshaufen N**	SD	**Seeschlacht N**	SD
2015	**434**	61	**191**	27
2016	**1875**	164	**276**	25
2017	**8144**	454	**255**	22
2018	**2629**	154	**274**	23
2019	**629**	55	**222**	28
2020	**171**	18	**167**	18
2021	**1516**	131	**128**	11
2022	**2468**	143	**71**	6

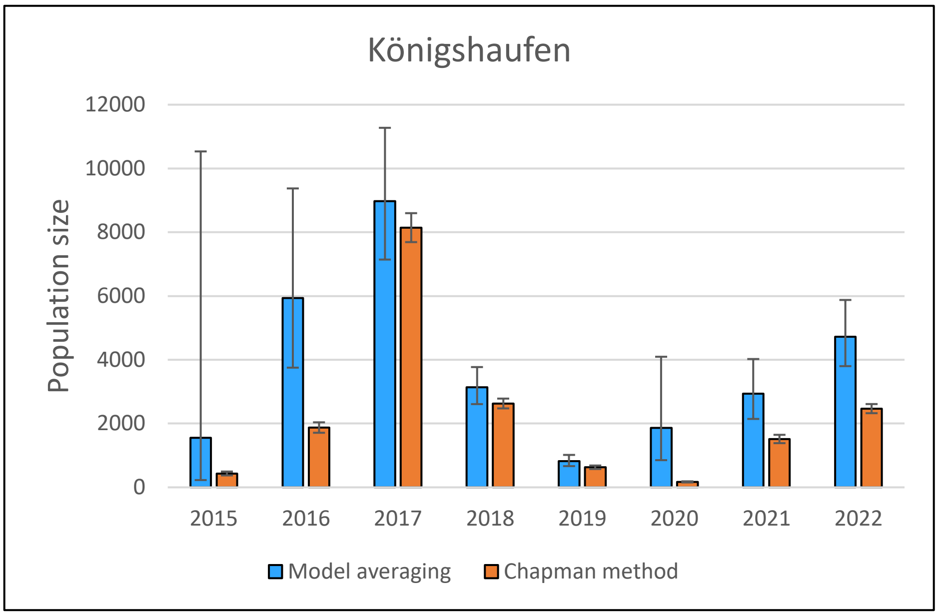

Fig. 25: Comparison of model averaged population size estimates from this study (blue) and estimates calculated with the Chapman modification of the Lincoln-Petersen index in Czurda et al. (2023) (orange) at Königshaufen for each study year. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R (model averaging) and the standard deviation (Chapman method).

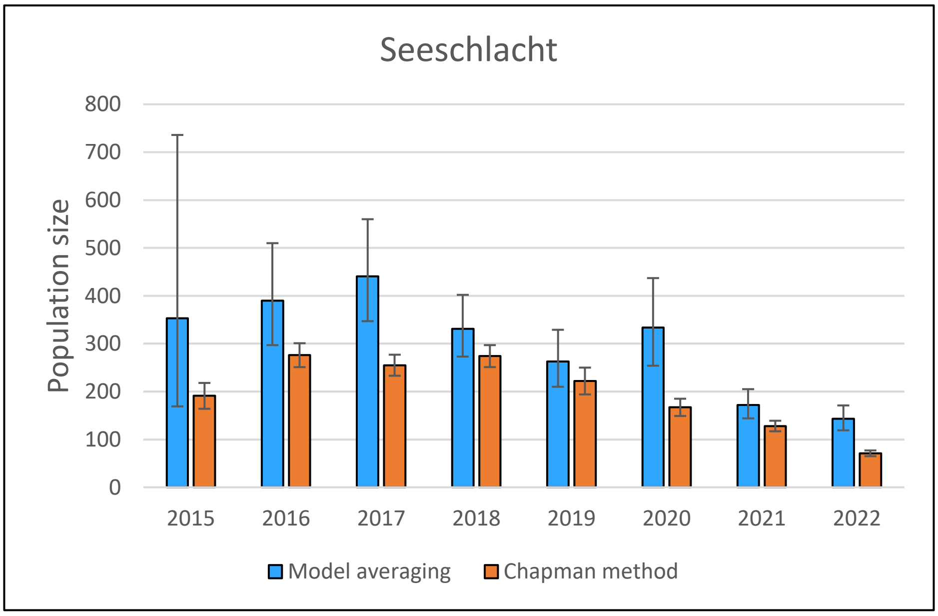

Fig. 26: Comparison of model averaged population size estimates from this study (blue) and estimates calculated with the Chapman modification of the Lincoln-Petersen index in Czurda et al. (2023) (orange) in Seeschlacht for each study year. Error bars show the 95% confidence intervals as calculated by the "openCR.fit" function of the openCR package in R (model averaging) and the standard deviation (Chapman method).

Life history variation

Apparent survival of adult fire-bellied toads was higher in Seeschlacht than at Königshaufen.

The low apparent survival of adults at Königshaufen may be a result of high mortality, high permanent emigration, or both, as the parameter apparent survival cannot separate mortality from permanent emigration (Ergon and Gardner 2014, Gilroy et al. 2012). Due to the stochastic water level fluctuations of the two ponds, individuals may migrate to other areas to avoid unfavourable environmental conditions. Evidence of migration was found in an earlier study, as metamorphs of 2008 were recaptured in 2009 in a water body on the opposite side of the dam (Philippi 2013).
Similar conclusions were drawn by Cayuela et al. (2016b) when studying the yellow-bellied toad, *Bombina variegata*. The authors found lower apparent survival for populations inhabiting more unpredictable than predictable habitats. Possible explanations for these differences were higher dispersal rates due to the unpredictability of breeding sites, and costs associated with dispersal. These results are supported by another study where the authors observed higher intra- and interannual dispersal rates in more unpredictable environments (Cayuela et al. 2016d).
Dispersal costs could also play a role at Königshaufen, as the two ponds are located close to a moderately frequented road on the opposite side of the dam that could cause road mortality of migrating toads.

Different predation pressures in each study area may also influence apparent survival. Königshaufen most likely attracts more and larger predators, as the number of potential prey items is much higher and more concentrated than in Seeschlacht. The two ponds also serve as breeding grounds for other amphibian species such as the Danube crested newt (*Triturus dobrogicus*), tree frogs (*Hyla arborea*), agile frogs (*Rana dalmatina*), water frogs (*Pelophylax esculentus* complex), or common spadefoot toads (*Pelobates fuscus*) (Gollmann 2016, Schedl et al. 2009). Predators such as grey herons (*Ardea cinerea*) (personal communication Günter Gollmann), and grass snakes (*Natrix natrix*), have been frequently sighted at Königshaufen. While adult *B. bombina* individuals are somewhat protected by their skin toxins, they can still end up as prey (see Gollmann et al. 2012).

Survival estimates for fire-bellied toads from other studies are scarce. Cogălniceanu and Miaud (2004) estimated an annual survival rate of 0.59 for a population inhabiting an island in the lower Danube floodplain of Romania. Environmental conditions were comparable to Königshaufen, with varying water levels due to at least two major flood events per year. In Denmark, survival rates of *B. bombina* ranged from around 0.5 to 0.9 depending on the intensity of surrounding agricultural activity (Briggs 1996).

The differences in apparent survival between Königshaufen and Seeschlacht can also be illustrated by the recapture frequencies of individuals and the number of years that had passed between first capture and last recapture event. Individuals in Seeschlacht were recaptured more frequently (Table 5) and reached considerably higher ages than those at Königshaufen (Fig. 27).

Similar results were found in other studies: Cogălniceanu and Miaud (2004) estimated an adult life expectancy of 2.9 years for the Romanian population. The oldest registered *B. bombina* individual was only five years old (Cogălniceanu and Miaud 2003). In Denmark, animals that reached eleven (Fog 1996) and twelve years (Briggs 1996) of age respectively were reported, in Russia, a maximum age of eleven years is stated (Ananjeva and Borkin 1979 in Gollmann et al. 2012). Due to the highly stochastic nature of the environment, the lifespans of fire-bellied toads inhabiting floodplains are severely reduced (Cogălniceanu and Miaud 2004).

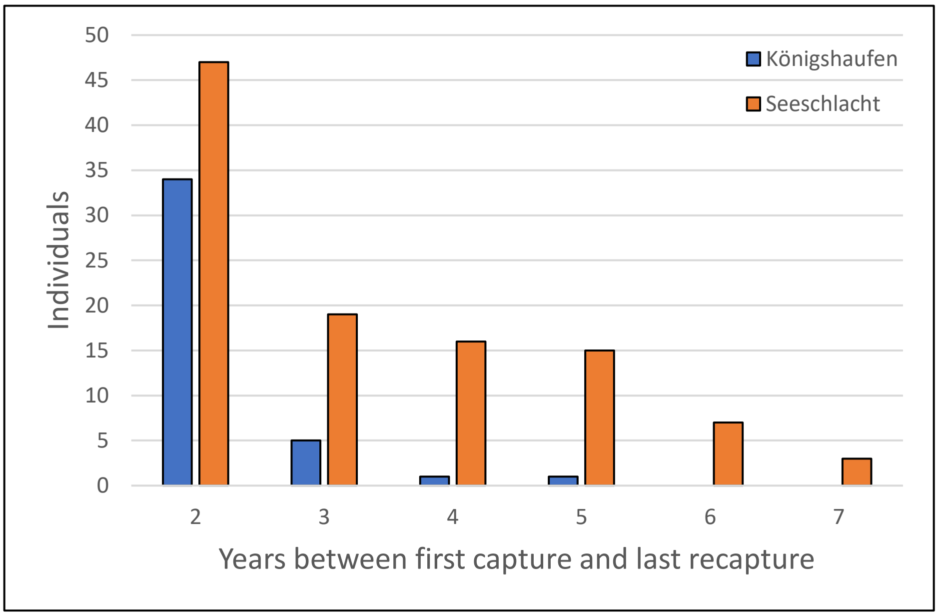

Fig. 27: Number of years between first capture and last recapture event of fire-bellied toads that were recaptured at least two years apart, separated per study area.

Apparent survival was lower for juvenile than for adult toads in Seeschlacht, and slightly higher at Königshaufen.

The lower apparent survival of juvenile compared to adult animals in Seeschlacht fall in line with observations from similar studies on the yellow-bellied toad (Cayuela et al. 2016a, 2016b, 2016c). These three studies investigated the effects of different environmental conditions (drought, spatiotemporal availability of breeding sites, and weather respectively) on populations of *B. variegata* and found lower apparent survival for juveniles than for adults for all tested scenarios.

At Königshaufen, the higher apparent survival for juvenile than for adult animals could be explained by the potentially high permanent emigration rates of adults.

It should also be noted that for the statistical models used in this study, the age-class “juvenile” was modelled as “sex”, however, the models are not designed for changing sexes. There were a number of cases in which the sex of juveniles that had been recaptured as adults changed from “j” to “m” or “f”. The model estimates the probability of individuals surviving from one primary session to the next. If an individual was classified as “j” in the first session, and as “a” in the second session, it counts towards apparent survival of juveniles. While the model can still use this information for calculations, apparent survival rates of juveniles should be interpreted with care.

Per capita recruitment of adult toads was higher at Königshaufen than in Seeschlacht.

The most important cause for these differences is the fact that productivity at Königshaufen is considerably higher than it is in Seeschlacht. There is strong evidence suggesting that the Königshaufen ponds are exceptionally well suited as breeding grounds for *B. bombina*, better than the water bodies of Seeschlacht: Metamorphs were found almost exclusively at Königshaufen and the number of encountered metamorphs greatly exceeded the number of captured ones during most of the studied years. The only registered metamorphs in Seeschlacht were from 2019 (15) and 2022 (2). While this may be a result of inadequate sampling, it is still a strong indicator of low reproductive output. Similar results were found in 2008, when numbers of metamorphs exceeded a thousand at Königshaufen, while only four were found in Seeschlacht (Philippi 2013). Another good indicator is the higher number of juvenile fire-bellied toads captured at Königshaufen during most study years (Table 4).
Schedl (2005) lists several factors that contribute to the suitability of water bodies as breeding grounds for *B. bombina* such as open water, sun exposure, submersed macrophytes, and medium- to larger sized water bodies. Frenz (2004) also showed that fire-bellied toads preferred temporary water bodies over more permanent ones. One of the Königshaufen ponds was also excavated at the beginning of the 1980s (Schratt-Ehrendorfer and Rotter 1999), which likely has increased its value as a breeding site by reducing the effects of terrestrialization.
In Seeschlacht, most of the water bodies do not fulfil the above-mentioned criteria for successful reproduction. In 2019, 13 of the 15 metamorphs were captured in water body number 5, which is one of the largest and more sun-exposed water bodies. The introduction of fish into another formerly suitable pond that could have served as the main spawning ground may have negatively impacted recruitment (Philippi 2013, Philippi and Gollmann 2014). Higher water levels can lead to the introduction of fish into nearby fish-free water bodies (Schedl et al. 2009).

While Königshaufen is more suited for reproduction, strong intra-annual water level fluctuations can pose a threat to reproduction if the ponds fall dry early, as shown by the low population size estimate for 2019 (Table 18, Fig. 21). Duration of egg and larval development of *B. bombina* takes two to three months depending on water temperatures (see review in Gollmann et al. 2012). Groundwater levels at Königshaufen (Fig. 7) suggest that water levels remained high enough for successful reproduction during most of the studied years. The high productivity during favourable years has also proved to be sufficient to compensate for years with higher reproductive failure. Toads may however have to adjust their timing of breeding activity from year to year. Breeding season lasts for several months and is influenced by solar radiation, temperature, or water levels (Gollmann et al. 2012). If environmental conditions are not favourable at the beginning of the season, females may be more likely to wait until conditions are more suitable.

Higher tadpole predation by predatory aquatic insects such as diving beetles (Dytiscidae) or the nymphs of dragonflies (Anisoptera) in Seeschlacht may also contribute to the low recruitment rates. Predation pressure is usually lower in temporary than in more permanent ponds, where predators such as different insect species can be found (Skelly 1997). To avoid desiccation, some aquatic insects migrate to more stable water bodies (Hershey et al. 2010). At Königshaufen, stochastic desiccation events lead to the reduced abundance of potential predators. Observations from Beranek et al. (2021) support this theory, as the authors found lower abundances of tadpole predators and higher metamorph output in wetlands with shorter hydroperiods, as opposed to wetlands with longer ones when studying the green and golden bell frog, *Ranoidea aurea*, in Australia. Similar results were reported by Loman (2002) who studied the common frog, *Rana temporaria*, in Sweden.

In addition to the above-mentioned factors, the low apparent survival of adult individuals at Königshaufen can also increase per capita recruitment: If apparent survival of adults is low and recruitment remains constant, the number of new adults entering the population per capita is higher.

Per capita recruitment of juveniles was slightly higher in Seeschlacht than at Königshaufen.

The higher per capita recruitment of juveniles in Seeschlacht can be explained by the fact that per capita recruitment is defined as the number of new entrants per class (juvenile, male, female) at time t scaled by 1/number of the same class in the population at time t – 1 (Efford 2022). Since the number of juvenile fire-bellied toads in Seeschlacht was low each year (Table 4), the per capita recruitment rate of new juveniles entering the population was slightly higher in Seeschlacht than at Königshaufen, where juveniles were far more abundant.

Potential additional factor contributing to the observed differences in life history traits.

Another possible, but more theoretical cause for the differences in life history traits between Königshaufen and Seeschlacht could be variation in resource allocation. Cogălniceanu and Miaud (2004) argue that the low life expectancy and limited growth of fire-bellied toads on an island in the lower Danube floodplain of Romania might, at least partly, be due to the high annual investment into reproduction. Compared to other studies, toads in the Romanian population were on average smaller and had shorter lifespans. Longevity and body length may therefore serve as an indicator of environmental variability on a gradient from disturbed floodplains to more stable environments (Cogălniceanu and Miaud 2003). The same may apply to the populations of Seeschlacht and Königshaufen. Due to the more dynamic water levels at Königshaufen, toads may invest more resources in early maturation and reproduction, leading to smaller body size and lower body mass, and therefore higher mortality. In Seeschlacht, the stable environmental conditions allow for greater investment in growth and somatic maintenance, resulting in larger body size and higher body mass, and thus an increased probability of survival, but lower reproductive output. The study from Briggs (1996) partly supports this theory, as he observed that fire-bellied toads produce only a small number of eggs when adult survival is high. Findings from Philippi (2013) suggest that there is a difference in body condition of toads between the two study areas, as the calculated scaled mass index of adults was lower at Königshaufen (“oil-harbour ponds”) than in Seeschlacht (“reed zone”) for the year 2008. The evaluation and comparison of morphometric data of fire-bellied toads from both study areas across the years could shed some more light on this subject.

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Supplementary material

Table A1: Overview of all capture events from the year 2015 combined and separated per date of sampling session and study site.

Date	Study site	Individuals	Capture events	Recaptures	Adults	Juveniles	Males	Females	Meta
22.04.2015	Königshaufen	29	29	0	5	24	4	1	0
24.04.2015	Seeschlacht	47	47	0	45	2	22	23	0
08.05.2015	Königshaufen	27	28	1	27	1	7	20	0
19.05.2015	Seeschlacht	21	27	6	27	0	15	12	0
03.06.2015	Seeschlacht	2	2	0	1	1	1	0	0
03.06.2015	Königshaufen	2	2	0	1	1	0	1	0
16.06.2015	Seeschlacht	1	1	0	1	0	1	0	0
25.06.2015	Königshaufen	15	15	0	14	1	6	8	0
	Total	**144**	**151**	**7**	**121**	**30**	**56**	**65**	0

Table A2: Overview of all capture events from the year 2016 combined and separated per date of sampling session and study site. Metamorphs (Meta) are not included in the numbers of individuals and capture events.

Date	Study site	Individuals	Capture events	Recaptures	Adults	Juveniles	Males	Females	Meta
31.03.2016	Seeschlacht	15	18	3	18	0	10	8	0
31.03.2016	Königshaufen	45	45	0	1	44	0	1	0
20.04.2016	Seeschlacht	31	37	6	37	0	20	17	0
21.04.2016	Königshaufen	95	97	2	40	57	15	25	0
11.05.2016	Seeschlacht	51	72	21	72	0	35	37	0
23.05.2016	Königshaufen	127	129	2	5	124	1	4	0
08.06.2016	Seeschlacht	31	42	11	39	3	20	19	0
16.06.2016	Königshaufen	92	100	8	47	53	26	21	0
24.06.2016	Seeschlacht	2	7	5	7	0	3	4	0
07.07.2016	Königshaufen	90	96	6	53	43	32	21	9
	Total	**579**	**643**	**64**	**319**	**324**	**162**	**157**	9

Table A3: Overview of all capture events from the year 2017 combined and separated per date of sampling session and study site. Metamorphs (Meta) are not included in the numbers of individuals and capture events.

Date	Study site	Individuals	Capture events	Recaptures	Adults	Juveniles	Males	Females	Meta
29.03.2017	Seeschlacht	8	8	0	4	4	1	3	0
29.03.2017	Königshaufen	235	241	6	40	201	26	14	0
10.04.2017	Königshaufen	310	326	16	116	210	44	72	0
04.05.2017	Königshaufen	242	273	31	65	208	41	24	0
12.05.2017	Seeschlacht	62	87	25	65	22	36	29	0
17.05.2017	Königshaufen	108	122	14	29	93	17	12	0
01.06.2017	Seeschlacht	33	63	30	50	13	24	26	0
30.06.2017	Seeschlacht	4	7	3	5	2	2	3	0
03.07.2017	Königshaufen	229	262	33	30	232	24	6	1
	Total	**1231**	**1389**	**158**	**404**	**985**	**215**	**189**	1

Table A4: Overview of all capture events from the year 2018 combined and separated per date of sampling session and study site. Metamorphs (Meta) are not included in the numbers of individuals and capture events.

Date	Study site	Individuals	Capture events	Recaptures	Adults	Juveniles	Males	Females	Meta
11.04.2018	Seeschlacht	35	59	24	44	15	24	20	0
18.04.2018	Königshaufen	192	227	35	105	122	60	45	0
24.04.2018	Seeschlacht	32	77	45	68	9	30	38	0
04.05.2018	Königshaufen	127	157	30	82	75	31	51	0
30.05.2018	Seeschlacht	12	30	18	29	1	12	17	0
07.06.2018	Königshaufen	187	231	44	134	97	64	70	0
15.06.2018	Seeschlacht	8	14	6	11	3	7	4	0
02.07.2018	Königshaufen	41	52	11	24	28	18	6	4
20.07.2018	Königshaufen	0	0	0	0	0	0	0	32
20.08.2018	Königshaufen	1	1	0	0	1	0	0	14
20.08.2018	Seeschlacht	4	9	5	8	1	4	4	0
	Total	**639**	**857**	**218**	**505**	**352**	**250**	**255**	50

Table A5: Overview of all capture events from the year 2019 combined and separated per date of sampling session and study site. Metamorphs (Meta) are not included in the numbers of individuals and capture events.

Date	Study site	Individuals	Capture events	Recaptures	Adults	Juveniles	Males	Females	Meta
03.04.2019	Seeschlacht	2	5	3	2	3	1	1	0
03.04.2019	Königshaufen	16	22	6	18	4	7	11	0
17.04.2019	Königshaufen	72	91	19	67	24	22	45	0
24.04.2019	Seeschlacht	23	46	23	41	5	20	21	0
08.05.2019	Königshaufen	54	88	34	69	19	18	51	0
22.05.2019	Seeschlacht	2	6	4	6	0	1	5	0
05.06.2019	Seeschlacht	15	31	16	27	4	10	17	0
07.06.2019	Königshaufen	8	16	8	15	1	4	11	0
12.06.2019	Königshaufen	34	43	9	40	3	15	25	0
19.06.2019	Seeschlacht	5	15	10	15	0	6	9	0
09.07.2019	Königshaufen	47	77	30	70	7	33	37	0
06.08.2019	Königshaufen	2	7	5	7	0	2	5	64
14.08.2018	Seeschlacht	1	10	9	10	0	1	9	15
	Total	**281**	**457**	**176**	**387**	**70**	**140**	**247**	79

Table A6: Overview of all capture events from the year 2020 combined and separated per date of sampling session and study site. Metamorphs (Meta) are not included in the numbers of individuals and capture events.

Date	Study site	Individuals	Capture events	Recaptures	Adults	Juveniles	Males	Females	Meta
03.06.2020	Seeschlacht	33	41	8	14	27	5	9	0
09.06.2020	Königshaufen	7	7	0	0	7	0	0	0
09.06.2020	Seeschlacht	7	14	7	5	9	4	1	0
16.06.2020	Seeschlacht	20	29	9	16	13	7	9	0
30.06.2020	Königshaufen	40	42	2	16	26	10	6	0
08.07.2020	Seeschlacht	16	32	16	17	15	5	12	0
21.07.2020	Königshaufen	36	40	4	29	11	16	13	1
12.08.2020	Seeschlacht	3	9	6	8	1	3	5	0
20.08.2020	Königshaufen	2	2	0	0	2	0	0	85
	Total	**164**	**216**	**52**	**105**	**111**	**50**	**55**	86

Table A7: Overview of all capture events from the year 2021 combined and separated per date of sampling session and study site. Metamorphs (Meta) are not included in the numbers of individuals and capture events.

Date	Study site	Individuals	Capture events	Recaptures	Adults	Juveniles	Males	Females	Meta
30.03.2021	Seeschlacht	7	11	4	6	5	2	4	0
30.03.2021	Königshaufen	37	37	0	1	36	0	1	0
27.04.2021	Königshaufen	21	25	4	1	24	0	1	0
04.05.2021	Seeschlacht	17	31	14	21	10	10	11	0
11.05.2021	Königshaufen	157	161	4	6	155	3	3	0
21.05.2021	Seeschlacht	15	37	22	26	11	11	15	0
01.06.2021	Königshaufen	89	102	13	5	97	1	4	0
08.06.2021	Seeschlacht	13	50	37	41	9	19	22	0
17.06.2021	Königshaufen	56	71	15	14	57	4	10	0
22.06.2021	Seeschlacht	7	48	41	39	9	15	24	0
06.07.2021	Königshaufen	57	67	10	21	46	17	4	0
13.07.2021	Seeschlacht	0	28	28	22	6	6	16	0
27.07.2021	Königshaufen	0	0	0	0	0	0	0	66
	Total	**476**	**668**	**192**	**203**	**465**	**88**	**115**	66

Table A8: Overview of all capture events from the year 2022 combined and separated per date of sampling session and study site. Metamorphs (Meta) are not included in the numbers of individuals and capture events.

Date	Study site	Individuals	Capture events	Recaptures	Adults	Juveniles	Males	Females	Meta
23.03.2022	Königshaufen	3	3	0	0	3	0	0	0
13.04.2022	Königshaufen	74	78	4	33	45	18	15	0
29.04.2022	Seeschlacht	8	32	24	26	6	9	17	0
04.05.2022	Königshaufen	190	209	19	78	131	35	43	0
11.05.2022	Seeschlacht	12	45	33	38	7	16	22	0
18.05.2022	Königshaufen	150	165	15	22	143	9	13	0
27.05.2022	Seeschlacht	4	27	23	24	3	11	13	0
01.06.2022	Königshaufen	202	237	35	33	204	17	16	0
08.06.2022	Seeschlacht	11	30	19	29	1	13	16	0
29.06.2022	Königshaufen	148	174	26	62	112	34	28	3
06.07.2022	Seeschlacht	3	22	19	21	1	8	13	0
27.07.2022	Königshaufen	16	21	5	1	20	1	0	64
03.08.2022	Seeschlacht	4	32	28	31	1	11	20	0
24.08.2022	Seeschlacht	1	23	22	20	3	5	15	2
	Total	**826**	**1098**	**272**	**418**	**680**	**187**	**231**	69