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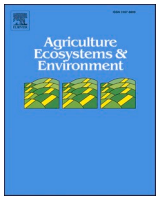

Use of agricultural fields by Natterjack toads: Implications for pesticide exposure

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ABSTRACT

Land sharing conservation strategies might not work if wildlife is exposed to plant protection products. Plant protection products are used to protect crops against harmful organisms yet they can also have unwanted side effects on non-target organisms. Amphibians are one group of non-target organisms for which there is evidence that plant protection products can have negative effects on individuals and populations. Despite much research on amphibian ecotoxicology, not much is known about the exposure of amphibians to plant protection products in agricultural landscapes. Here, we study habitat use and movement behaviour of an endangered amphibian, the Natterjack toad *Epidalea calamita*, in two study areas in Switzerland. We placed arrays of artificial cover boards in agricultural fields and adjacent non-agricultural habitats and used a photographic mark-recapture approach to track individual toads, both adults and juveniles, during and after the reproductive season in the terrestrial habitat. We used multistate and spatial mark-recapture models to analyse the data. Toads used the agricultural fields during spring and summer and set up their home ranges within the fields but there was a great turnover of individuals. Toad densities were higher in agricultural fields than other habitat types, including a nature reserve suitable for the species. Toads preferred open soils and avoided grassy meadows typical of agricultural set-asides, suggesting that the conservation of the species in agricultural landscapes requires new types of biodiversity promotion areas. The results of the study show that toads use agricultural fields during most of the growing season and are thus likely to be exposed to plant protection products.

1. Introduction

Animals are well known to use agricultural areas as habitats (Fischer et al., 2012). However, if agriculture becomes too intense, biodiversity is lost from the agricultural landscape (Donald et al., 2001, Arntzen et al., 2017, Rigal et al., 2023). There is an ongoing debate whether land sharing approaches are better than land sparing for the conservation of biodiversity in agricultural landscapes (Green et al., 2005, Fischer et al., 2014). Land sparing means that some areas are used for intensive agriculture whereas others are set aside for biodiversity conservation. Under a land sharing strategy, a reduced agricultural intensity allows wildlife to use the agricultural area as habitat. Both strategies may work and have their advantages and disadvantages. Land sharing approaches can be compromised if sharing means that wildlife are exposed to harmful effects from plant protection products (PPPs). There is a large body of evidence that PPPs can harm and kill non-target organisms and ultimately contribute to the decline of biodiversity in agricultural landscapes, neighbouring nature reserves, and other remnants of natural habitat (Davidson et al., 2002, Geiger et al., 2010, Brühl et al., 2011, Beketov et al., 2013, Weltje et al., 2013, Hallmann et al., 2014, Tscharntke et al., 2021). Given that the benefits of biodiversity conservation must be weighed against the economic costs of reducing the use of PPPs (e.g., yield loss; Seufert and Ramankutty, 2017), it is important to better understand the effects of PPP use on wildlife (Köhler and

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Triebskorn, 2013, Leeb et al., 2020, Churko et al., 2024).

Amphibians are undergoing population declines at a global scale (Houlahan et al., 2000, Stuart et al., 2004, Hof et al., 2011) and PPPs are thought to be one of the drivers (Collins and Storfer, 2003, Hayes et al., 2006, Brühl et al., 2013). This is because amphibians commonly occur in agricultural landscapes (Knutson et al., 2004, Arntzen et al., 2017, Savic et al., 2021, Valdez et al., 2021). The effect of PPPs depends on both toxicity and exposure, i.e., the ability of a product to damage an organism as well as how much and for how long an organism is subjected to the product. PPP toxicity and modes of action have been well studied in amphibians, but exposure is not as well-described (Aldrich et al., 2016). An important challenge to a more complete understanding of ecotoxicology in this group of animals is their use of both aquatic and terrestrial habitats. PPPs are regularly detected in aquatic breeding sites, and there is evidence of PPP-mediated population declines (Davidson et al., 2002, Relyea, 2005, Brühl et al., 2013, Smalling et al., 2015, Goessens et al., 2022). Far less is known about exposure to PPPs in the terrestrial habitat, though exposure is likely (Lenhardt et al., 2013, Leeb et al., 2020, Geissen et al., 2021), and it is here where they may be directly exposed to PPPs by overspray or other pathways.

To understand potential exposure in the terrestrial environment, and to develop suitable counter measures, we need to advance our understanding of how amphibians use agricultural landscapes (Wagner et al., 2014, Aldrich et al., 2016, Weltje et al., 2018, Renoirt et al., 2021). Precise knowledge of how, when, and which species of amphibians use cropland and neighbouring associated habitats is lacking. Ockleford et al. (2018) list 38 out of 47 European amphibian species as likely to occur on croplands, but the degree and patterns of their use are diverse. Many of these species exhibit preferences for off-crop habitat and only cross cropland during seasonal migrations or dispersal events (Churko et al., 2024), but even such limited use can strongly coincide with the application of PPPs (Berger et al., 2013, Lenhardt et al., 2014, Leeb et al., 2020). Spatial patterns of use change over the course of the season and in different landscapes (Indermaur et al., 2009, Schweizer, 2016, Swanson et al., 2018). Different crops, their management, and their spatial relationship to alternative habitats can all also influence the attractiveness of cropland to amphibians (Lenhardt et al., 2013, Hansen et al., 2019). Thus, it is important to identify major factors determining when and where a given species may occur in an agricultural landscape.

Here, we aim to contribute to a better understanding of the terrestrial habitat use of amphibians in an agricultural landscape. We studied the use of agricultural fields by the Natterjack toad, *Epidalea calamita*. Natterjack toads are known to use agricultural landscapes (Schwabe, 1977, Miaud and Sanuy, 2005), were suggested as a model species for amphibian ecotoxicology (Ockleford et al., 2018), and are declining in many parts of Europe (Dufresnes and Perrin, 2015, Cruickshank et al., 2016, Albero et al., 2021). We use a mark-recapture approach using artificial cover boards (Denton and Beebee, 1992, Sutherland et al., 2016) to assess survival, space use and movement in two study regions containing Natterjack toad breeding sites embedded within mosaics of cropland, biodiversity promotion areas (BPA; also known as agricultural set asides; the aim is to promote biodiversity in farmland) and nature reserves dedicated to amphibian conservation. Over the three-year study, we investigate how toad activity differs in each major land use type, with changing weather and crop types, and across sex and age groups. This will help to judge factors that influence their usage patterns and how much time the toads spend in in-crop and off-crop habitats.

2. Methods

2.1. Study sites

The study was carried out in northern Switzerland in two locations: Lachmatt (canton Basel-Landschaft) from 2020 to 2022, and Wauwil (canton Lucerne) from 2021 to 2022. Large Natterjack toad populations are present at both locations and are known to frequent the agricultural fields (personal communication with farmers).

The study area in Lachmatt (Fig. S1) includes the southern part of a neighbouring nature reserve. Encouraged by yearly plowing, the nature reserve largely consists of open, stone and gravel ground cover with pioneer vegetation and contains five man-made depressions where rain-fed temporary ponds, the pond type preferred by the Natterjack toad, can form. To the west and south of the nature reserve lies a mixture of cropland, meadow, and pasture, interspersed with meadowed BPAs containing man-made ponds. The western crop field was used to grow lentils in the first year, after which it was used as an intensive meadow for the following years. In the southern field, beans, rapeseed and maize were grown in each year, respectively.

The Wauwil study area is comparatively more representative of intensive agriculture, with large field sizes and only a limited presence of natural habitats in the direct vicinity. Two study areas, about 1 km apart, were used for data collection in Wauwil (described as the northwest (NW) and southeast (SE) ponds, respectively; Fig. S1). The two areas were each centred around a meadow with man-made ponds surrounded by agricultural fields. At the NW pond, this meadow was a BPA, while the meadow at the SE ponds is protected as a nature reserve. Despite this, we called the SE meadow a BPA in our analysis since it was functionally identical to the other BPAs in our study. Maize was grown on all fields in the first year; in the second year, wheat, rye and barley. The BPA in the northwest also includes a newly planted hedge with open loose soil at its base.

2.2. Study design

The study sites were divided into different survey zones and categorized according to the following land use types: 'Cropland', 'BPA' and 'Nature reserve' (Table S1). Within each zone, we placed cover boards (Denton and Beebee, 1992) in groups of five in a line, or following the perimeter of small ponds, at a distance of ~1 m from each other. By deploying the boards in clusters of five, we could effectively simulate larger structures like logs or woodpiles while retaining ease of management. In the cropland, the boards were placed at varying, regular distances to the field margins. In the other land use types, we placed them within or next to different microhabitats if present (e.g., the BPA at the NW pond in Wauwil had sets of boards near the breeding pond, the hedge, and in the meadow). We used 3 cm thick, untreated 3-ply pinewood, cut to 30 cm×60 cm rectangles for coverboards. At this size, the boards were easily manoeuvrable and could be placed between crop rows without reducing the farmer's yield. We also placed a layer of sawdust under all boards to minimize the effect of differences in the ground cover under the boards across land use types, and to increase attractivity to toads. Sawdust buffers against extreme temperatures, retains moisture longer after precipitation and is suitable as a burrowing substrate for toads (Lange et al., 2020).

2.3. Data collection

We made daytime surveys of the two study sites two times per week over the course of the Natterjack toad's active period. In 2020, the study period was 20 April to 9 September; in 2021, from 23 April to 4 October. In 2022, the study period was shortened due to project constraints, from 30 April to 31 August (though the peak activity period of the toads had passed). Each board was carefully lifted and the habitat underneath was searched for amphibians. For each amphibian we found, we recorded the species and location, and, if it was a Natterjack toad, we determined their sex and age class, measured their mass (to 0.1 g) and dorsal length (to 0.1 cm), and photographed their dorsum (camera: Samsung Galaxy S10; ambient lighting with no direct sunlight). Natterjack toads were divided into three age categories based on dorsal length: Adult (> 50 mm), subadult (40–50 mm) or juvenile (< 40 mm). Sex was determined in adult individuals by the colour of their throat: males have a bluish-red tinge, while female throats are pale and white. Using ESRI's

ArcGIS Survey 123 mobile app (ESRI, 2021), we created a record for each encounter linking individual IDs and all associated data to board location, and integrated the spatial dataset directly into ArcGIS Pro (ESRI, 2020).

2.4. Individual identification

To identify Natterjack toad individuals within the study populations, we analysed the encounter photographs using the pattern recognition software Wild-ID (Bolger et al., 2012). The program makes pairwise comparisons of all photographs, and scores all potential matches according to their similarities. The user then visually reviews up to 20 of the top scoring matches to manually confirm or reject them. Since the user works in sequential order, only comparing a photo to those that came before, it is only necessary to determine a single match before moving onto the next photo. Repeated captures of the same individual are then aggregated together after working through the dataset. All photos were first cropped, reoriented, and resampled to a resolution width of 1000 pixels so that all toads were framed identically, minimizing this source of noise in the analysis. Thanks to the Natterjack toads' distinctive yellow dorsal line, which varies in length, thickness, and consistency with every individual, matching pairs could be quickly identified and the manual review was completed within a few hours.

2.5. Weather data

For the capture recapture analyses, we examined the potential influence of weather on toad activity over the study period. All meteorological data was obtained from MeteoSwiss (via https://gate.meteoswiss.ch/idaweb/), including total precipitation per hour, soil temperature, and air humidity as 10-minute averages. From these, we calculated daily means along with daily maximum and minimum temperatures. As a surrogate for soil humidity, we also examined the influence of precipitation over longer timespans of three days and two weeks, respectively. The data from the Muttenz Schweizerhalle weather station, located ~1 km from the study area, was used for the Lachmatt study area. For Wauwil, we used data from the Kottwil weather station, which is 1.10 km away from the SE Ponds, and 1.80 km from the NW Pond. As the computation time of both capture recapture models substantially increases with each additional variable, we only included weather-related variables in the final set of candidate models if they were significantly correlated (Pearson's correlation test) with the total number of toads encountered per survey.

2.6. Data analysis

2.6.1. Multistate capture recapture

Using the capture (i.e. encounter) histories of unique individuals provided by the WildID program, we conducted multistate capture-recapture analyses (Lebreton et al., 2009) for each location pooled across study years. The package RMark (Laake, 2013) in R (R Core Team, 2020) was used for this. In addition to the capture history of an individual, multistate capture-recapture models include information on the respective 'state' or condition in which an animal was (re)captured to investigate the state's influence on descriptive parameters of the study population. These parameters include the survival rates (S) and detection probabilities (p) within each of the states that individuals can be found, as well as the transition rates (psi) between them. In a closed study system, where individuals cannot move in or out of the study environment, the probability of survival strictly reflects mortality rates in each state. In open systems such as our study sites, where individuals are free to move in and out of the study area, the probability of survival reflects both mortality and emigration and they cannot be distinguished between.

Like all mark-recapture models (Schmidt et al., 2002), multi-state capture-recapture models make several basic assumptions that can be violated by animal behaviour, including the absence of any trap dependency among the animals and the absence of transient individuals within the study site (Genovart and Pradel, 2019). Before building potential models, we performed goodness-of-fit tests of these assumptions on the capture histories of the identified toads using the R2ucare R package (Gimenez et al., 2018). Trap dependency arises when encountered animals return to the traps (in our case to the boards) disproportionately often or infrequently. This increases or decreases the probability of detection of such animals. Transience arises when recaptured and newly captured animals are not recaptured to the same extent, but a disproportionately large number of animals disappear after being captured once and are no longer recaptured (Pradel et al., 1997; Genovart and Pradel, 2019). Possible reasons for this are differences between age groups, since young animals, for example, can have an increased mortality rate and therefore disappear disproportionately after the first catch. Animals with a large radius of activity could also stray from the study area. This behaviour lowers the estimated probability of survival. If the capture history dataset exhibits violations of these assumptions, the models must be fitted with additional covariates to control for their influence. Transience, for example, can potentially be addressed by grouping captures by age class. Alternatively, differentiating captures between the first and all subsequent recaptures allows testing for trap awareness (Pradel and Sanz-Aguilar, 2012).

For this study, we focused on investigating the influence of anthropogenic land use on the survival, detection, and transition rates of encountered individuals. Land use type was modelled as our main state of interest (i.e., stratum) and categorized as 1 = Nature reserve, 2 = BPA and 3 = Cropland (Table S1). Survival and detection probabilities in the set of candidate models varied by land use type (landuse), initial capture vs recapture (capturebin), sex (sex), days since the start of the study period (time), year (year), age class (age), and rainfall in the last three days or two weeks (rain3d and rain2w), and combinations thereof. Transition rates between land use types varied only by land use in all models. Model performance was evaluated based on the small-sample corrected Akaike Information Criteria (AICc). To perform the full analysis across all years at each site, we only considered data from the study period that was common to each year. The standardized study period across all years was mid-May – mid-August and produced capture histories for each unique individual across 30 visits at the Lachmatt site, and 33 at Wauwil. This removed the late season sampling period in 2021 from the analysis.

2.6.2. Spatial capture-recapture

To develop a more accurate picture of the density of the study populations, and the approximate size of their home ranges, we also performed a spatial capture-recapture (SCR) analysis using the R Package oSCR (Schmidt et al., 2017, Sutherland et al., 2019). SCR analyses differ from traditional capture-recapture models in that the activity centres of study individuals moving within their home ranges are included in the modelling process. This allows the creation of spatially explicit predictions of detection probabilities, which vary across the landscape based on the distance of a trap (or, cover board) to each individual's activity centre. With this information, animal density can be estimated across the entire study area and across various spatial covariates.

Again, we focused on examining the importance of anthropogenic land use in determining Natterjack toad presence, testing the effect of land use type on toad density (d) and detection probability (p). To examine differences in model estimates across age class (adults and subadults vs. juveniles) and sex, we ran two sets of models. In the first set, all individual capture histories were included, and detection rate and sigma (activity centre size) were allowed to vary with age class. In the second set, we focussed on adult toads, excluding all individuals without a determined sex, and allowed p and sigma to vary with sex. For both model sets, detection probability was allowed to vary with trap-awareness (b), which behaves similarly to the 'capturebin' variable by structuring the capture histories into toads that have never been caught

before and those that have been caught at least once. We also considered the influence of the following covariates: study year, distance of the board cluster to the nearest breeding pond, distance to the margin of the sample zone, and rainfall in the last three days and in the last two weeks. We assessed 128 models generated from combinations of the following covariates: (*d ~ 1, year, landuse, distPond, distMargin; p ~ 1, b, year, landuse, sex, age, rain3d, rain2w; sigma ~ 1, year, sex, age*).

We ran separate models for Wauwil and Lachmatt and divided the study years into separate 'sessions' (sessions are sub-models that allow spatial input data to vary with a factor of interest, like year or region; Sutherland et al., 2019). The 'state space' (the area encompassing all possible centres of activity of the encountered individuals) was defined as the smallest concave polygon containing all boards, buffered by a distance of 1.5 times the mean maximum distance moved (mmdm) observed across the recaptured individuals. The analysis was performed with a resolution of 10 m in Lachmatt, and 5 m in Wauwil. To reduce computing time, the boards within a cluster were combined into a single point located at the centre of the cluster.

3. Results

3.1. Overview of encounter history

3.1.1. Lachmatt

We encountered 1695 amphibians over three study seasons in Lachmatt, of which 1217 were Natterjack toads. We also observed 328 Alpine newts (*Ichthyosaura alpestris*), 45 Common toads (*Bufo bufo*), 3 Water frogs (*Pelophylax* aggr.), 1 Palmate newt (*Lissotriton helveticus*), and 1 Common frog (*Rana temporaria*). With the exception of the boards around the ponds in the nature reserve, these other amphibians rarely made use of our shelters. Of the 1217 Natterjack toads, 1133 were found under boards and a further 84 under natural hiding places. The number of observations of Natterjack toads varied greatly across years, with an overwhelming number of records occurring in the 2021 field season (Fig. 1a). The summers of 2020 and 2022 were hot and dry, and the temporary ponds used by the Natterjack toads for breeding in the area never held water for longer than a few weeks (Fig. 1b). Juvenile recruitment in these years was near zero and adults and subadults made up the majority of encountered individuals (Fig. 1c). On the other hand, rainfall was nearly continuous in the late spring and early summer of 2021. The various small pools throughout the study area were always full, and even a section of the southern crop field was flooded for multiple weeks. In September and October, we observed an extreme increase in toad presence due to the emergence of multiple cohorts of juveniles from the ponds (Figs. 1,2). We recorded 726 juveniles in 2021, 92% of all encounters that year. After their metamorphosis and emergence, the young toads lingered around the ponds from which they came in the BPAs and nature reserve, appearing to take refuge in the structure-rich habitat surrounding them.

We found the majority of toads in the crop fields and the nature reserve (Figs. 1d,2), though there were strong differences between adults and juveniles with regard to the use of the boards in each land use type. Adult and subadult Natterjack toads were found more frequently in the fields than in the BPAs or the nature reserve. Juveniles were common in all zones, but their numbers were highest in the nature reserve. Over the three seasons and across all sites, nearly all Natterjack toad observations were made under boards placed on open ground cover (soil, sand, or gravel). The end of the 2021 season is an exception, however, where we frequently found juveniles in the grassy and gravel-covered zones.

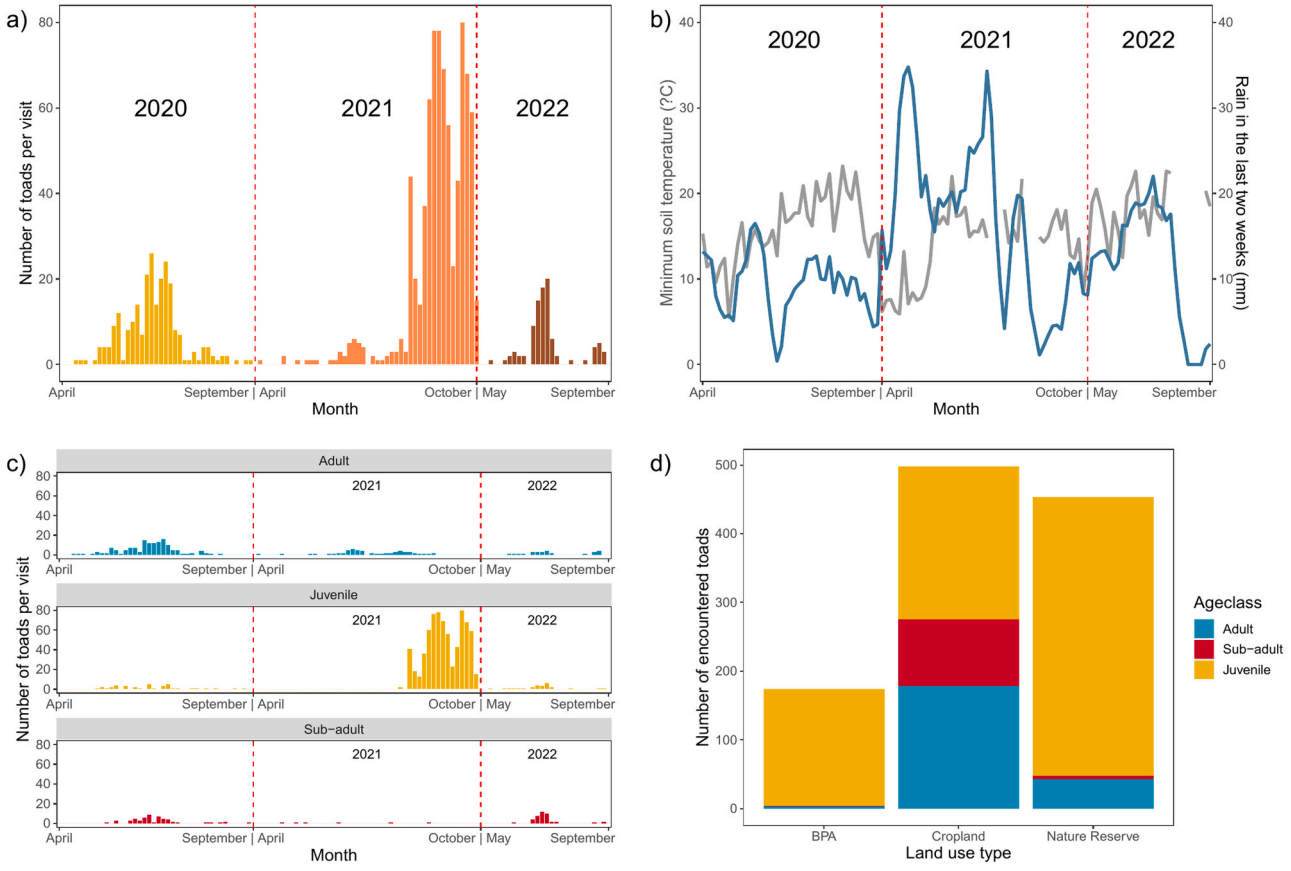

Fig. 1. Number of Natterjack toad observations in Lachmatt over the three study years in total (a), and split by age class (c). Panel b shows the course of precipitation and minimum soil temperature over the same time period. Panel d summarizes the number of toad encounters by land use type and age class, with adults shown in teal, sub-adults in red, and juveniles in yellow.

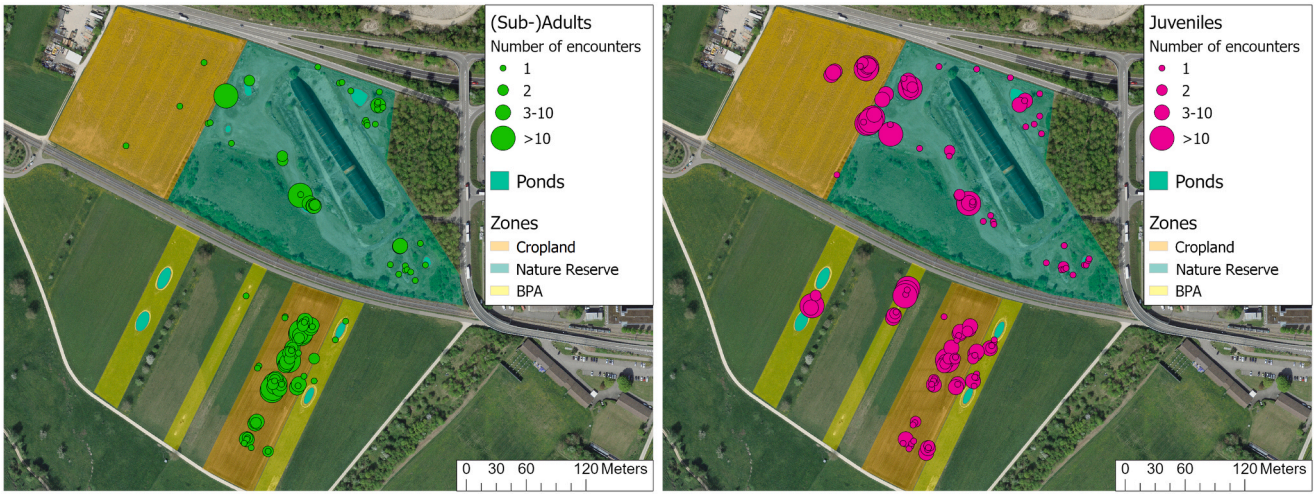

Fig. 2. Spatial overview of the occurrence of all recorded adult and subadult (green circles above) and juvenile (pink circles below) Natterjack toads from 2020 to 2022 in Lachmatt, BL. The size of the circles scales with the number of toads found at the respective locations. Map background: swissimage © swisstopo.

3.1.2. *Wauwil*

Over the two study years in Wauwil, we observed 522 Natterjack toads. Of these, 503 were sighted under boards and 19 under natural hiding places or on open ground. In contrast to the Lachmatt site, we observed few amphibians of other species: water frogs (*Pelophylax* aggr.) occasionally used the boards adjacent to the ponds at the South-East location and there was a single sighting of a common toad (Bufo bufo).

In both years, Natterjack toad observations increased in early May as temperatures rose (Fig. 3ab). In 2021, the number of toad observations per visit peaked in June and July. The summer saw ample rainfall with no long periods of drought. Like in Lachmatt, juvenile recruitment was high, as is reflected by the increase in the number of juveniles we encountered at the tail end of the 2021 season, and the disproportionate number of juveniles observed at the start of the 2022 field season

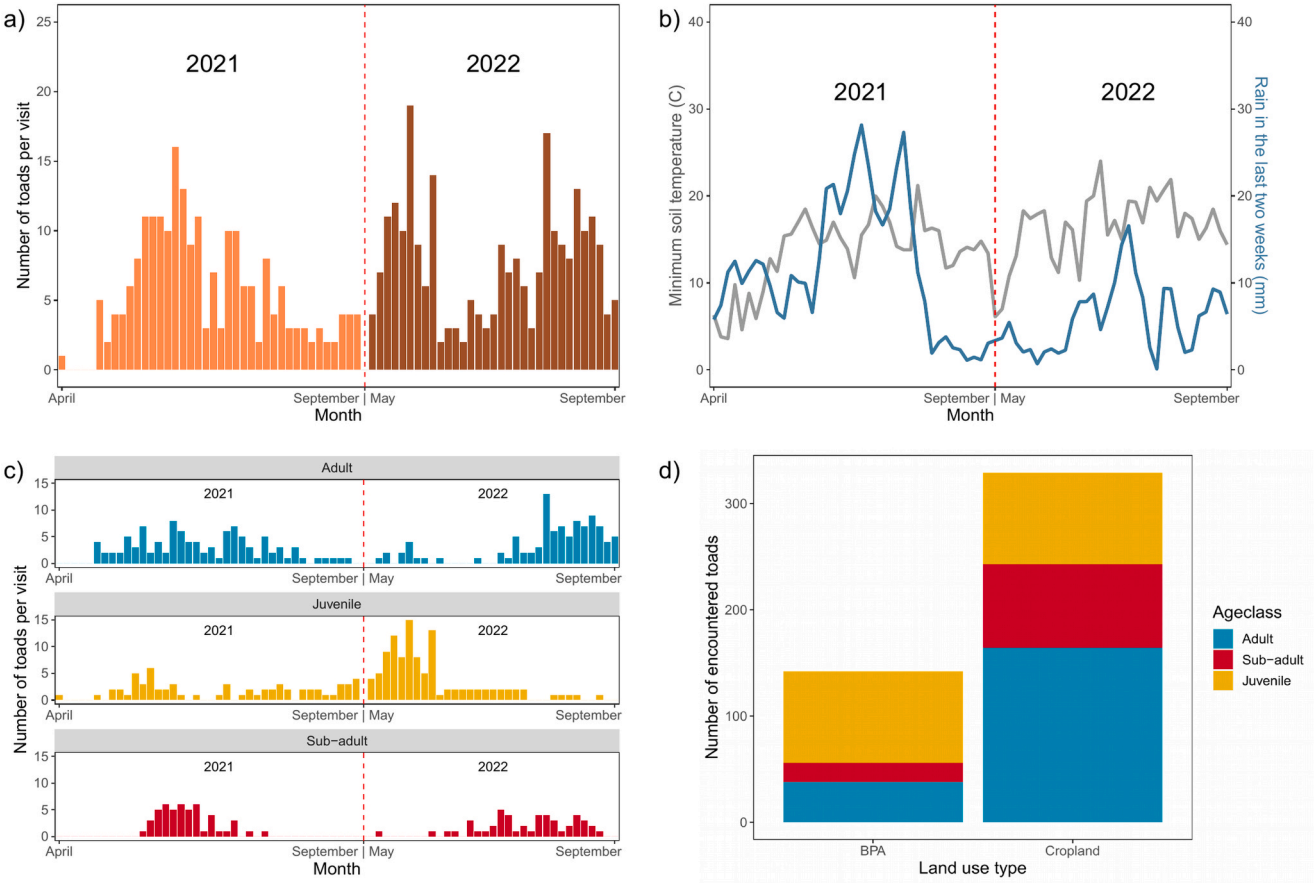

Fig. 3. Number of Natterjack toad observations in Wauwil over the three study years in total (a), and split by age class (c). Panel b shows the course of precipitation and minimum soil temperature over the same time period. Panel d summarizes the number of toad encounters by land use type and age class, with adults shown in teal, sub-adults in red, and juveniles in yellow.

(Fig. 3c). In 2022, toad encounters quickly decreased with continued dry weather through the early summer. Following a sequence of mid-summer rain showers, a second peak of toad observations occurred in August 2022.

We encountered Natterjack toads under boards in all land use types, though the majority were located in the crop fields (Figs. 3d,4). A key exception was a small hedge structure east of the pond in the BPA at the Northeast site (Fig. 4). This hedge, freshly planted and surrounded by open loose soil, was a hot spot for Natterjack toads throughout the study period (127 of 139 toad encounters).

Only nine out of 503 total toad encounters occurred at boards situated on ground cover other than open soil, indicating a clear bias against board usage in vegetated areas. This behaviour was reflected in the use of boards in the crop fields over the course of the two growing seasons. In 2021, boards in the open maize fields were heavily used by toads at the beginning of the season. As the maize grew taller and weeds denser, toad encounters skewed towards the hedge structure in the BPA. In the second season, we saw an opposite temporal pattern. The start of the Natterjack toad active season coincided with densely developed grain fields. Board use within the fields was strongly reduced compared to 2021. Board use in the fields only began to increase once the grain had been harvested.

3.2. Multistate capture recapture

3.2.1. Goodness-of-fit tests

The overall goodness-of-fit tests for Lachmatt and Wauwil showed a lack of fit. In Wauwil, this was due to a significantly positive test for transience (Table S2). The positive sign test indicates a surplus of animals that were seen once and never again in the dataset (Gimenez et al., 2018). Transience was also observed in the Lachmatt population as well as a significant test for trap dependency. The sign test for 'trap dependency' was negative, indicating 'trap happiness', an excess of animals that repeatedly return to the cover boards, causing inflated recapture rates (Pradel and Sanz-Aguilar, 2012).

To correct for these patterns, we included 'capturebin' as an explanatory variable for survival and detection rate in all examined multi-state models. The 'capturebin' variable differentiates the capture events of each individual between the first and all subsequent recaptures, allowing separate estimates of survival and detection rate for transient and/or trap-unaware individuals versus resident and/or trap-aware individuals.

3.2.2. Best models

Across all evaluated models in both study regions, land use was always included as a covariate for survival probability and detection probability in the best-ranking models. Distinguishing between potential transient toads and residents with the 'capturebin' variable also

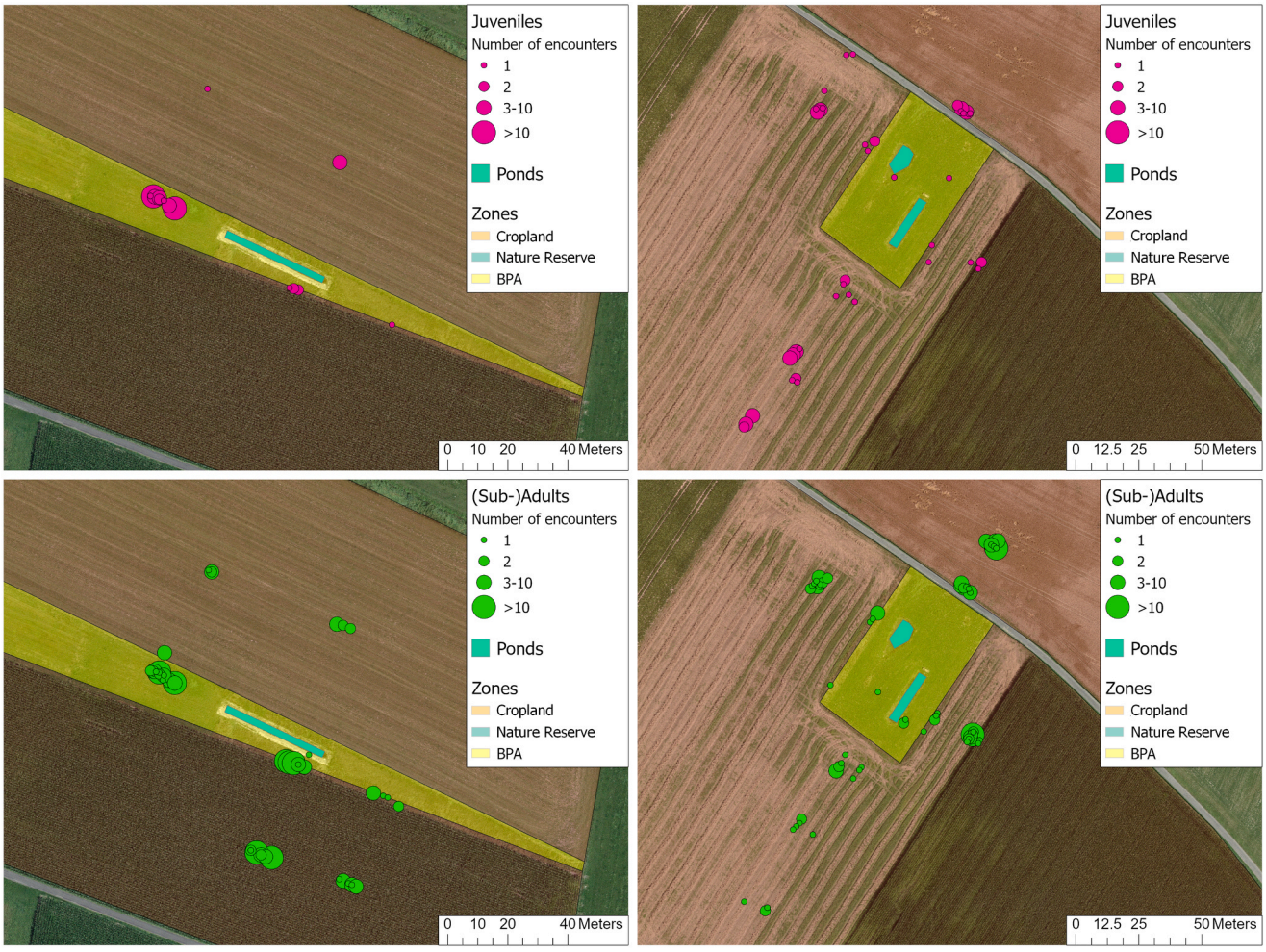

Fig. 4. Spatial overview of the occurrences of all recorded adult and subadult toads (green circles, above) and juvenile toads (pink circles, below) in the years 2021 and 2022 at the two locations in Wauwil, LU. Left: the northwest location; Right: the southeast location. The size of the circle scales with the number of toads found at the respective location. Map background: swissimage © swisstopo.

proved an important determinant of survival probabilities at both sites, with transients having markedly reduced survival probabilities as compared to the recaptured toads. Likewise, rainfall was a driver of detection probability in both regions, with longer-term rainfall over the last two weeks being positively correlated with toad presence under the boards. We attribute this to the emergence of crevices in the soil as it dries over extended periods without rain. The crevices offer readily available shelter for the toads and there is little incentive to use our boards. Transition rates varied between different habitat zones, but were generally very low (<10%) with a few exceptions.

3.2.3. Lachmatt

In Lachmatt, the best model consisted of the combined effects of land use and the first and all remaining captures (capturebin) on survival rate, while land use, sex, age, and rainfall determined detection probability (Table 1). Survival probabilities across land use zones were similar amongst recaptured toads (S1, 0.81–0.96), but differed greatly between the two capturebin categories, with recaptured individuals showing much higher survival probabilities. Survival probabilities among potential transients (S0) were lowest in the nature reserve (0.30) and highest within cropland zones (0.68). Detection probability was extremely low (<1%) in the BPAs in comparison to the other zones for all sex and age classes. Juvenile toads had the lowest probability of being detected, while male adults were more likely to use our boards than females. No toads encountered in the nature reserve were reencountered in another area of the study region resulting in estimated movement rates of zero between the nature reserve and all other zones. On the other hand, some toads encountered in the south-east crop field were also found on other occasions under boards in the adjacent BPA. The model predicted a moderate amount of exchange between the crop fields and BPAs, with movement weighted towards the BPA.

3.2.4. Wauwil

The best model for Wauwil consisted once again of land use and capturebin for survival probabilities, with land use, sex, and rainfall driving detection probabilities (Table 2). When compared within the same capturebin, survival probabilities were higher in the BPAs versus cropland (0.99, 95% CI [0.966–0.997] vs. 0.86, 95% CI [0.819–0.907]).

Female and male toads had similar detection probabilities in either zone (BPA 0.72; cropland 0.23), but individuals with no identified sex (juveniles and subadults) had markedly reduced probabilities of being detected. In contrast to the results from Lachmatt, detection probability was higher in the BPAs across all sexes as compared to in the crop fields. We also saw an opposite trend in transition rates, where the exchange of toads between zones was more strongly weighted away from the BPAs.

3.3. Spatial capture-recapture

The best SCR models across the age- and sex-based models in Lachmatt and Wauwil were generally similar (Table S3). Land use and year were included as covariates for toad density in all models, and for detection rates in nearly all, with the exception of year in the age-based Wauwil model. Trap dependence, b, and rainfall were also important determinants of detection probability in all models. Activity centre sizes (sigma) were generally driven by study year, with the exception of sex in the sex-based model in Wauwil. We found no patterns in toad density relative to the distance of boards to field margins or breeding sites.

Density estimates could not be estimated accurately for three of the four models, including both age-based models (Fig. 5a). From the successful sex-based model for Lachmatt, we see that adult toad density was significantly higher in croplands than in BPAs (0.1–0.2 toads per 10 m2 in cropland vs. near zero in BPAs; Fig. 5b). Adult toad density increased two-fold in 2022, likely due to the high juvenile recruitment of 2021. Male and female toad density were approximately the same in the two land use zones.

Estimated detection probabilities in the SCR models were consistent across study regions (Figs. 5,6). Detection probabilities in BPAs were similar to those in cropland. Board use by adults was generally higher than by juveniles. In Lachmatt, males were also more like to use the boards than females. Detection probabilities were between 0.05 and 0.3, indicating that we were on average sampling between 1/20th and 1/3rd of available toads in the study regions. One exception is the age-based model for the 2021 field season in Lachmatt, where detection probabilities increased sharply. Rainfall was an important predictor of detection rates in all models, with cumulative rainfall over the two weeks before a visit being included in the best models for three of the

Table 1
Results from the best multi-state capture-recapture model for Lachmatt, BL across all years (2020–2022): *S(~landuse + capturebin) p(~landuse + sex + ageclass + rain2w) Psi(~-1 + landuse:tolanduse)*, *S* = survival rate, *p* = detection probability, *Psi* = transition rate, *capturebin* = initial capture (S0) vs all recaptures (S1), *landuse* = land use type, *ageclass* = sub(adults) vs juveniles. Estimates indicate average rates per data collection period across the study period. SE = standard error, LCL/UCL = lower and upper limits of the 95% confidence interval.

Parameter	Land use type	Capture-bin	Sex	Age Class	Estimate	SE	LCL	UCL
Survival	Nature Reserve	S0			0.298	0.048	0.214	0.398
(S)	Nature Reserve	S1			0.828	0.043	0.726	0.898
	BPA	S0			0.498	0.192	0.181	0.817
	BPA	S1			0.919	0.052	0.744	0.978
	Cropland	S0			0.676	0.061	0.548	0.782
	Cropland	S1			0.96	0.021	0.892	0.986
Detection	Nature Reserve		female	(sub)adult	0.285	0.078	0.157	0.458
(p)	BPA		female	(sub)adult	0.002	0.002	0.001	0.01
	Cropland		female	(sub)adult	0.579	0.07	0.44	0.707
	Nature Reserve		male	(sub)adult	0.453	0.074	0.315	0.598
	BPA		male	(sub)adult	0.005	0.004	0.001	0.02
	Cropland		male	(sub)adult	0.742	0.056	0.617	0.836
	Nature Reserve		unknown	(sub)adult	0.503	0.143	0.248	0.754
	BPA		unknown	(sub)adult	0.006	0.005	0.001	0.027
	Cropland		unknown	(sub)adult	0.778	0.078	0.59	0.895
	Nature Reserve		unknown	juvenile	0.103	0.038	0.049	0.206
	BPA		unknown	juvenile	0.001	0.001	0	0.003
	Cropland		unknown	juvenile	0.286	0.067	0.174	0.432
Transitions	Nature Reserve > BPA				0	0	0	0
(Psi)	Nature Reserve > Cropland				0	0	0	0
	BPA> Nature Reserve				0	0	0	0
	BPA> Cropland				0.026	0.016	0.007	0.085
	Cropland > Nature Reserve				0	0	0	0
	Cropland > BPA				0.265	0.047	0.184	0.365

Table 2
Results from the best multi-state capture-recapture model for Wauwil, LU across all years (2021–2022): *S(~landuse + capturebin) p(~landuse + sex + rain2w) Psi(~-1 + landuse:tolanduse)*, *S* = survival rate, *p* = detection probability, *Psi* = transition rate, *capturebin* = initial capture (S0) vs all recaptures (S1), *landuse* = land use type. Estimates indicate average rates per data collection period across the study period. SE = standard error, LCL/UCL = lower and upper limits of the 95% confidence interval.

Parameter	Land use type	Capture-bin	Sex	Estimate	SE	LCL	UCL
Survival (S)	BPA	S0		0.839	0.085	0.604	0.947
	BPA	S1		0.99	0.006	0.966	0.997
	Cropland	S0		0.254	0.027	0.204	0.311
	Cropland	S1		0.869	0.022	0.819	0.907
Detection	BPA		female	0.726	0.086	0.531	0.86
(p)	Cropland		female	0.23	0.051	0.145	0.344
	BPA		male	0.72	0.073	0.558	0.84
	Cropland		male	0.225	0.03	0.172	0.289
	BPA		unknown	0.393	0.064	0.276	0.523
	Cropland		unknown	0.068	0.018	0.04	0.112
Transitions	BPA > Cropland			0.209	0.047	0.131	0.316
(Psi)	Cropland > BPA			0.018	0.005	0.01	0.032

datasets (Fig. 6). Increased rainfall increased the likelihood of toads being found under our cover boards. Additionally, the models consistently suggested extreme differences in detection probabilities with trap-awareness (Fig. 6). Detection probabilities for toads that had never been encountered before were estimated at nearly zero.

The mean maximum distance moved was similar across study regions, ranging from 38.6 to 48.6 m. Toad activity centre size was most strongly influenced by study year, ranging from 12 to 50 m depending on the year and peaking across most models in the rainy 2021 field season. Estimated home range sizes (based on a 95% space use area calculated as $\pi * 5.99 * sigma^2$) ranged from 0.27 ha to 4.7 ha. There were few differences in the size of toad activity centres relative to age or sex, though adult males were estimated to have larger home ranges in the Wauwil population (Fig. 5). The importance of study year in the models, and higher sigma values in 2021, suggests that rainfall increases the activity of Natterjack toads. In direct contrast to the results of the adults-only model, sigma was actually lower in 2021 in the age-based Lachmatt model, but this is a dataset dominated by juvenile records. While no significant difference was found between the sigma values of adults and juveniles in either age-based model, this contradictory pattern also hints at juveniles having smaller activity centres.

4. Discussion

The results of this study provide an in-depth analysis of the use of an agricultural landscape by an endangered amphibian, the Natterjack toad (Epidalea calamita). The results describe patterns of habitat use which have implications for the conservation of the species in agricultural landscapes where it is commonly exposed to PPPs (Churko et al., 2024).

Multiple habitat types were available to the toads. We did not detect much movement between the habitat types, suggesting that adult toads selected home ranges during the summer months, as was shown for ecologically similar toad species (Indermaur et al., 2009). They did not move from one habitat type to another. This result is confirmed by the fact that the goodness of fit test for the mark-recapture models detected 'trap happiness'. 'Trap happiness' is a technical term from the mark-recapture literature that describes animals that are found more often than expected under theoretical expectations (Schmidt et al., 2002). This is an indication that toads used the cover boards as shelter during the day in their home ranges, as they use deposits of woody debris as daytime shelter in natural habitats (Indermaur and Schmidt, 2011).

These results confirm previous reports that found that at least a subset of the population uses agricultural fields as terrestrial habitat after the breeding season (Miaud and Sanuy, 2005, Schweizer, 2016). While some toads apparently have chosen habitat types other than cropland (Miaud and Sanuy, 2005), we found that densities in cropland can be higher than in neighbouring habitat types (0.1–0.2 toads per 10 m^2; Fig. 5). However, there is also evidence that individual toads did not stay for long periods in the fields. First, while the estimates of survival are high (group S1 in Table 3), these estimates describe the intervals between checks of coverboards. Cumulative survival across multiple checks is low (i.e., the estimate of survival raised to the power of the number of checks, $survival^{\#checks}$). Mark-recapture estimates of survival are estimates of apparent survival, i.e., the product of true survival and site fidelity (Holenweg-Peter, 2001, Schmidt et al., 2017). True low survival in cropland is an unlikely explanation because survival was similar in other habitat types, e.g., the nature reserve. Thus, the more likely explanation is permanent emigration from the cover board arrays where toads were captured. This suggests that toads may set up home ranges for a while in the cropland (leading to the 'trap happiness' phenomenon), but will later move to other places. Further evidence for short residence times comes from the goodness of fit test of the mark-recapture models which detected transients. The test shows that there are, in comparison to binomial expectations, too many individuals which were captured only once (Schmidt et al., 2002). Several biological processes can lead to transients (Genovart and Pradel, 2019). In the context of our study, two processes are likely. First, some toads show nomadic behaviour, e.g., invasive cane toads in Australia (Schwarzkopf and Alford, 2002), or Fowler's Toads in Canada (Jreidini and Green, 2022). Strong variation among individuals in movement behaviour are not uncommon in amphibians (Denoel et al., 2018). A second, not mutually exclusive, explanation may be related to home range size. Variation in home range size was fairly large in our study, ranging from 0.27 ha to 4.7 ha. Such strong variation among individuals was previously observed in Natterjack toads and other toads (Indermaur et al., 2011, Schweizer, 2016). The larger home ranges may have only partially overlapped with our cover board arrays. Thus, the toads with small home ranges may be those which showed 'trap happy' behaviour whereas the ones with larger home ranges were only rarely encountered within our study area, leading to the presence of transients in the goodness of fit tests. In any case, home range size is related to habitat quality (Indermaur et al., 2009) and implies that some toads have to move around more than other individuals. Taken together, toad densities can be high in agricultural fields but there appears to be a high turnover of individuals. This behaviour contrasts with the results of Schweizer (2016)'s radio telemetry study, which reported that Natterjack toads stayed in agricultural fields for long periods. Variation among populations in space use and movement behaviour could be due to variation in habitat quality (e.g., food availability; Indermaur et al., 2009, Sinsch et al., 2012).

Adults and juvenile toads differed in habitat use. While adults and subadults were mainly found in cropland, juveniles were found relatively equally in all habitat types (Figs. 1d and 2d). From our observations, juveniles tended to emerge from their breeding ponds after metamorphosis and fan out in all directions, indiscriminately taking

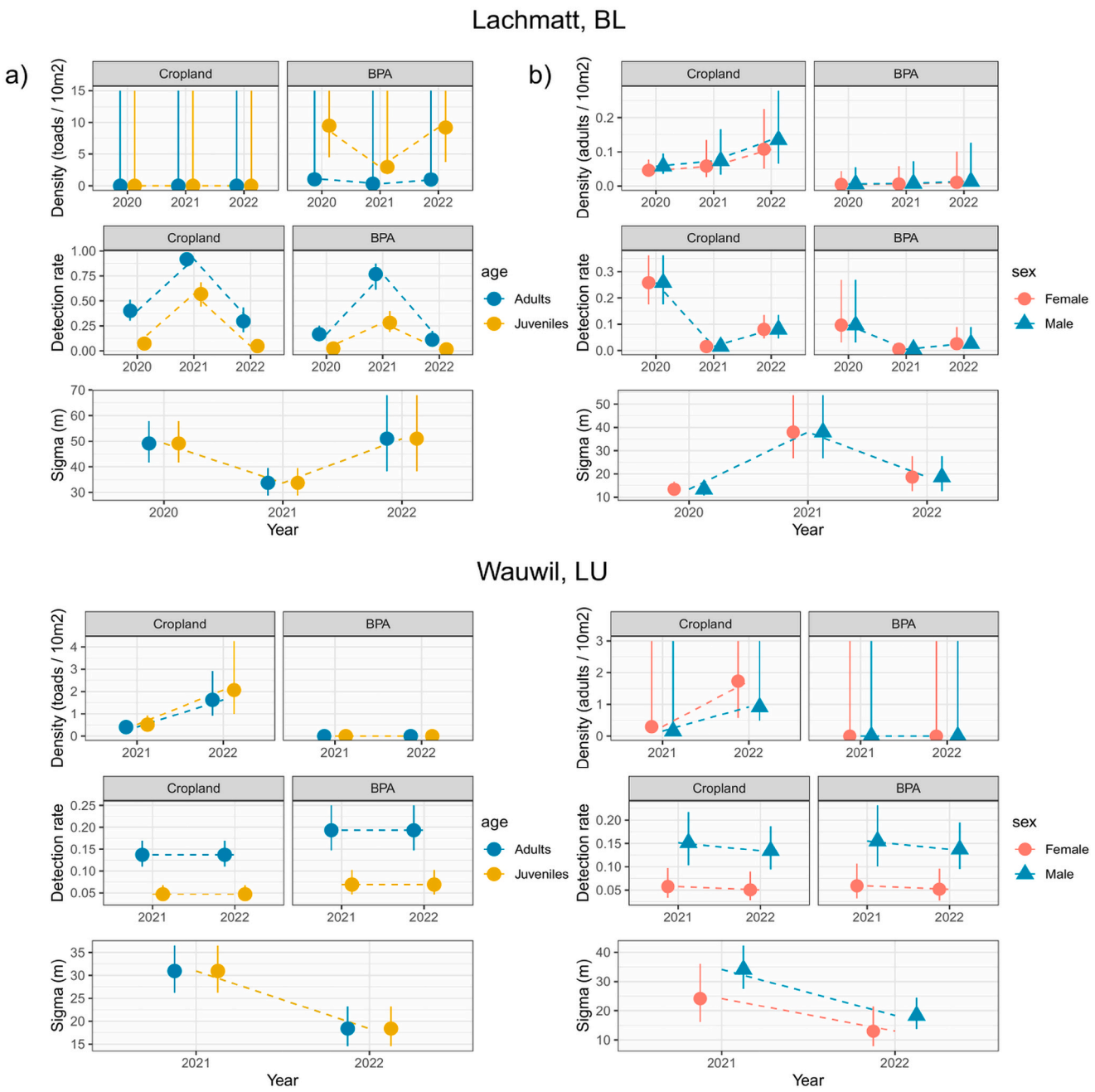

Fig. 5. Density and detection rate estimates in cropland vs. BPAs, and estimates of activity centre sizes (sigma) from the best spatial capture-recapture models for Lachmatt (above) and Wauwil (below). The left set of panes (a) shows the parameter estimates for the age-based models, with adults shown in teal and juveniles in yellow. The right set of panes (b) shows the estimates for the adult-only sex-based models, with females in red, and males in blue. Results from each field year are indicated along the x-axis in each panel.

shelter wherever they could find it. Adult Natterjack toads were more selective, predominantly using habitats with open, earthy or gravelly substrates and avoiding the grass-dominated BPAs, as expected given their preference for early successional habitats (Sinsch, 2009, Siffert et al., 2022).

The avoidance of grass-dominated BPAs by the toads in our study is an important insight. Biodiversity promotion areas in Swiss agriculture typically take the form of extensive meadows and flower strips as their creation and management requires little investment from the farmers. Our findings suggest that alternative types of BPAs may be necessary if the goal is to promote the Natterjack toad. The attractiveness of the Wauwil BPA with a hedge surrounded by open, disturbed soil suggests that toad usage of BPAs can be significantly increased by the inclusion of such microhabitats. Open ground could be discussed as a measure to specifically promote or protect adult Natterjack toads. Adult Natterjack toads use cropland throughout the season, from April to October. The open, loose soil provides them with a suitable habitat for hunting and hiding (Schweizer, 2016). From our observations, it is noticeable that fields in wide rows and loose vegetation (e.g., maize) are populated significantly more densely by Natterjack toads than fields with dense vegetation, such as wheat. A wheat field, which was part of the field study in 2022, did not record a single Natterjack toad sighting until the grain was harvested. After harvesting, Natterjack toads were suddenly found under the boards in the middle of the field. This example shows that dense vegetation could act as a barrier for Natterjack toads (Stevens et al., 2004). The choice of suitable planting could therefore already

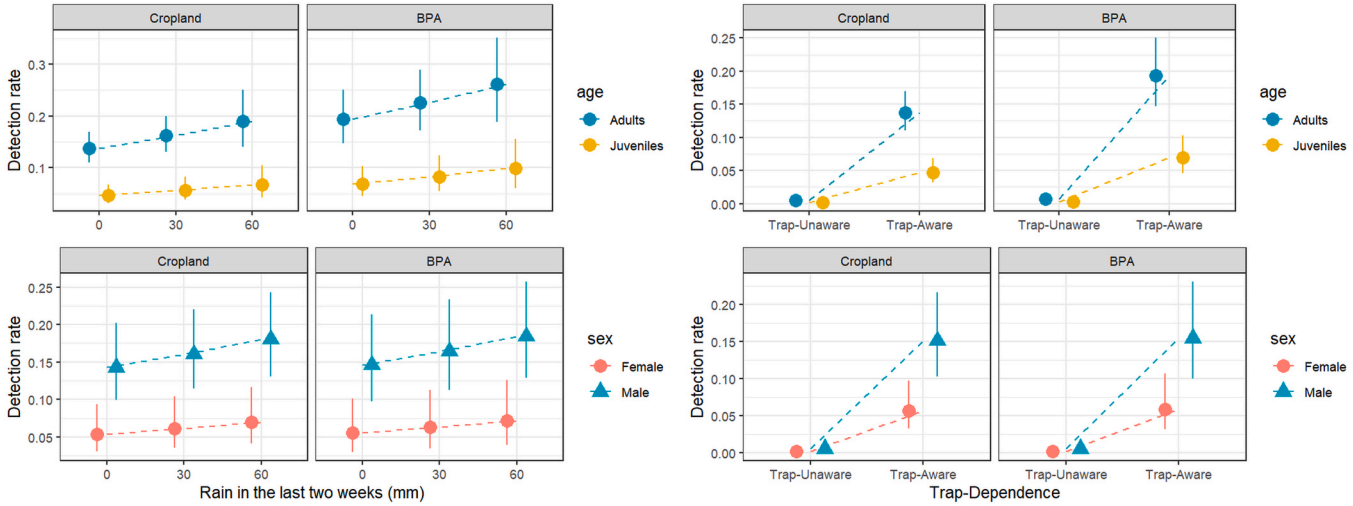

Fig. 6. Influence of cumulative rainfall (left) and trap-awareness (right) on detection rates in the Wauwil study population. The rainfall plots were generated by back-transforming model estimates for detection rate at three quantities of cumulative rainfall, 0, 30, and 60 mm. The top panes show the parameter estimates for the age-based models, with adults shown in teal and juveniles in yellow. The bottom panes show the estimates for the adult-only sex-based models, with females in red, and males in blue.

create additional habitat for Natterjack toads. Alternatively, it could be used to lure the Natterjack toads from the fields to the BPAs. The provision of open, loose soil on BPAs combined with plentiful microstructures for shelter could encourage adult Natterjack toads to spend more time in the BPAs where they would be less exposed to threats from PPPs or mechanical soil processing.

Our results show that Natterjack toads can be found during and after the breeding season in spring and summer in agricultural fields. Densities in fields can be higher than in adjacent habitat types. This implies that a large proportion of the population, both adults and juveniles, can be exposed to PPPs during the spring and summer months. Toads often use shelters where they are protected against direct overspray but Schweizer (2016) showed that many toads do not use shelters and do not dig themselves into the ground. Instead, they remain on the soil surface, particularly when the crop has grown to a certain size and plant root growth makes it impossible for the toads to dig into the soil. Thus, toads may be subjected to direct overspray if PPPs are not precisely applied to the crop plants. Mortality induced by PPPs could negatively affect population viability, particularly if juveniles are affected (Stevens and Baguette, 2008, Di Minin and Griffiths, 2011, Petrovan and Schmidt, 2019).

Risk assessment of PPPs is a lengthy and time-consuming process requiring international collaboration and multi-level acceptance among various approval authorities. In the face of widespread amphibian population declines, the implementation of mitigation measures that can be expected to protect or promote amphibians regardless of PPP approval is a sensible approach. Our work suggests that providing hiding places in fields or at their edges can be a beneficial promotional measure for the Natterjack toad. These can be piles of branches, for example, as they are an important hiding place for toads (Indermaur and Schmidt, 2011). The more branch piles there are, the smaller the home ranges of the toads (Indermaur and Schmidt, 2011), so less cropland is used by the toads. In addition to offering hiding places, our results show that it can be useful to offer other areas with open soil as an alternative to cropland, as this is a preferred microhabitat of toads. If such mitigation measures are not possible because, for example, farmers are opposed to it or open soils lead to an increased emergence of weeds, then other mitigation strategies could be considered. Mitigation strategies that compensate for, rather than reduce the risk of, pesticide exposure may be equally viable. Empirical and modelling studies suggest that the viability and size of Natterjack toad populations depend crucially on the availability of suitable ponds for reproduction (Beebee et al., 1996). Bozzuto and Schmidt (2024) found that provisioning additional ponds in a landscape was more beneficial to a theoretical metapopulation of Natterjack toads than reducing either the toxicity of or their exposure to PPPs. Thus, there may be multiple pathways towards a coexistence of agricultural production and amphibian conservation.

CRediT authorship contribution statement

Genoveva Haibach: Writing – review & editing, Investigation, Formal analysis, Data curation, Methodology. **Gregory Churko:** Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Benedikt R. Schmidt:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Erich Szerencsits:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Moritz Bär:** Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109049.

References

Albero, L., Martínez-Solano, Í., Arias, A., Lizana, M., Bécares, E., 2021. Amphibian metacommunity responses to agricultural intensification in a Mediterranean landscape. Land 10, 924. https://doi.org/10.3390/land10090924.

Aldrich, A., Junghans, M., Aeberli, C., Brühl, C.A., Streissl, F., Schmidt, B.R., 2016. Amphibians and plant-protection products – what research and action is needed? Environ. Sci. Eur. 28, 17. https://doi.org/10.1186/s12302-016-0085-6.

Arntzen, J.W., Abrahams, C., Meilink, W.R.M., Iosif, R., Zuiderwijk, A., 2017. Amphibian decline, pond loss and reduced population connectivity under agricultural intensification over a 38 year period. Biodivers. Conserv. 1411–1430. https://doi.org/10.1007/s10531-017-1307-y.

Beebee, T.J.C., Denton, J.S., Buckley, J., 1996. Factors affecting population densities of adult Natterjack toads *Bufo calamita* in Britain. J. Appl. Ecol. 33, 263–268.

Beketov, M.A., Kefford, B.J., Schäfer, R.B., Liess, M., 2013. Pesticides reduce regional biodiversity of stream invertebrates. Proc. Nat. Acad. Sci. USA 110, 11039–11043.

Berger, G., Graef, F., Pfeffer, H., 2013. Glyphosate applications on arable fields considerably coincide with migrating amphibians. Sci. Rep. 3, 2622. https://doi.org/10.1038/srep02622.

Bolger, D., Morrison, T., Vance, B., Lee, D., Farid, H., 2012. A computer-assisted system for photographic mark-recapture analysis. Methods Ecol. Evol. 3, 813–822.

Bozzuto, C., Schmidt, B.R., 2024. Effekte von Pflanzenschutzmitteln auf Populationen und Meta-populationen von Amphibien: Ergebnisse eines Modells für Kreuzkröten. Laubfrosch und Kammmolch. Agroscope Sci. 178 https://doi.org/10.34776/as178g.

Brühl, C.A., Pieper, S., Weber, B., 2011. Amphibians at risk? Susceptibility of terrestrial amphibian life stages to pesticides. Environ. Toxicol. Chem. 30, 2465–2472.

Brühl, C.A., Schmidt, T., Pieper, S., Alscher, A., 2013. Terrestrial pesticide exposure of amphibians: an underestimated cause of global decline? Sci. Rep. 3, 1135.

Churko, G., Szerencsits, E., Aldrich, A., Schmidt, B.R., 2024. Spatial analysis of the potential exposure of amphibians to plant protection products at the landscape scale. Basic Appl. Ecol. 76, 14–24. https://doi.org/10.1016/j.baae.2024.02.004.

Collins, J.P., Storfer, A., 2003. Global amphibian declines: sorting the hypotheses. Divers. Distrib. 9, 89–98.

Cruickshank, S.S., Ozgul, A., Zumbach, S., Schmidt, B.R., 2016. Quantifying population declines based on presence-only records for Red List assessments. Conserv. Biol. 30, 1112–1121.

Davidson, C., Shaffer, H.B., Jennings, M.R., 2002. Spatial tests of the pesticide drift, habitat destruction, UV-B, and climate-change hypotheses for california amphibian declines. Cons. Biol. 16, 1588–1601.

Denoel, M., Dalleuer, S., Langrand, E., Besnard, A., Cayuela, H., 2018. Dispersal and alternative breeding site fidelity strategies in an amphibian. Ecography 41, 1543–1555.

Denton, J.S., Beebee, T.J.C., 1992. An evaluation of methods for studying Natterjack toads (*Bufo calamita*) outside the breeding season. Amphib. -Reptil. 13, 365–374.

Di Minin, E., Griffiths, R.A., 2011. Viability analysis of a threatened amphibian population: modelling the past, present and future. Ecography 34, 172-169.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. R. Soc. Lond. Ser. B: Biol. Sci. 268, 25–29. https://doi.org/10.1098/rspb.2000.1325.

Dufresnes, C., Perrin, N., 2015. Effect of biogeographic history on population vulnerability in European amphibians. Cons. Biol. 29, 1235–1241.

ESRI, 2020. ArcGIS Pro: Release 2.6.3. Environmental Systems Research Institute, Redlands.

ESRI, 2021. ArcGIS Survey 123: Release 3.12.232. Environmental Systems Research Institute, Redlands.

Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G., von Wehrden, H., 2014. Land Sparing versus land sharing: moving forward. Conserv. Lett. 7, 149–157. https://doi.org/10.1111/conl.12084.

Fischer, J., Hartel, T., Kuemmerle, T., 2012. Conservation policy in traditional farming landscapes. Conserv. Lett. 5, 167–175. https://doi.org/10.1111/j.1755-263X.2012.00227.x.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl. Ecol. 11, 97–105.

Geissen, V., Silva, V., Lwanga, E.H., Beriot, N., Oostindie, K., Bin, Z., Pyne, E., Busink, S., Zomer, P., Mol, H., Ritsema, C.J., 2021. Cocktails of pesticide residues in conventional and organic farming systems in Europe - legacy of the past and turning point for the future. Environ. Pollut. 278, 116827.

Genovart, M., Pradel, R., 2019. Transience effect in capture-recapture studies: The importance of its biological meaning. PLoS One 14, e0222241. https://doi.org/10.1371/journal.pone.0222241.

Gimenez, O., Lebreton, J.D., Choquet, R., Pradel, R., 2018. R2ucare: An R package to perform goodness-of-fit tests for capture–recapture models. Methods Ecol. Evol. 9, 1749–1754. https://doi.org/10.1111/2041-210X.13014.

Goessens, T., De Baere, S., Deknock, A., De Troyer, N., Van Leeuwenberg, R., Martel, A., Pasmans, F., Goethals, P., Lens, L., Spanoghe, P., Vanhaecke, L., Croubels, S., 2022. Agricultural contaminants in amphibian breeding ponds: Occurrence, risk and correlation with agricultural land use. Sci. Total Environ. 806, 150661.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the Fate of Wild Nature. Science 307, 550–555. https://doi.org/10.1126/science.1106049.

Hallmann, C.A., Foppen, R.P.B., van Turnhout, C.A.M., de Kroon, H., Jongejans, E., 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature 511, 341–343.

Hansen, N.A., Scheele, B.C., Driscoll, D.A., Lindenmayer, D.B., 2019. Amphibians in agricultural landscapes: the habitat value of crop areas, linear plantings and remnant woodland patches. Animal conservation 22 (1), 72–82.

Hayes, T.B., Case, P., Chui, S., Chung, D., Haeffele, C., Haston, K., Lee, M., Mai, V.P., Marjuoa, Y., Parker, J., Tsui, M., 2006. Pesticide mixtures, endocrine disruption, and amphibian declines: are we underestimating the impact? Environ. Health Perspect. 114, 40–50. https://doi.org/10.1289/ehp.8051.

Hof, C., Araujo, M.B., Jetz, W., Rahbek, C., 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature 480, 516–519.

Holenweg-Peter, A.-K., 2001. Survival in adults of the water frog *Rana lessonae* and its hybridogenetic associate *Rana esculenta*. Can. J. Zool. 79, 652–661.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L., 2000. Quantitative evidence for global amphibian population declines. Nature 404, 752–755.

Indermaur, L., Gehring, M., Wehrle, W., Tockner, K., Naef-Daenzer, B., 2009. Behavior-based scale definitions for determining individual space use: requirements of two amphibians. Am. Nat. 173, 60–71.

Indermaur, L., Schmidt, B.R., 2011. Quantitative recommendations for amphibian terrestrial habitat conservation derived from habitat selection behavior. Ecol. Appl. 21, 2548–2554.

Jreidini, N., Green, D.M., 2022. Dispersal without drivers: Intrinsic and extrinsic variables have no impact on movement distances in a terrestrial amphibian. Ecol. Evol. 12, e9368.

Knutson, M.G., Richardson, W.B., Reineke, D.M., Gray, B.R., Parmelee, J.R., Weick, S.E., 2004. Agricultural ponds support amphibian populations. Ecol. Appl. 14, 669–684.

Köhler, H.-R., Triebskorn, R., 2013. Wildlife ecotoxicology of pesticides: can we track effects to the population level and beyond? Science 341, 759–765.

Laake, J., 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep. 2013-01, Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA. http://www.afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf.

Lange, L., Brischoux, F., Lourdais, O., 2020. Midwife toads (*Alytes obstetricans*) select their diurnal refuges based on hydric and thermal properties. Amphib. -Reptil. 41, 275–280.

Lebreton, J.D., Nichols, J.D., Barker, R.J., Pradel, R., Spendelow, J.A., 2009. Modeling individual animal histories with multistate capture–recapture models. Adv. Ecol. Res. 41, 87–173.

Leeb, C., Brühl, C., Theissinger, K., 2020. Potential pesticide exposure during the post-breeding migration of the common toad (*Bufo bufo*) in a vineyard dominated landscape. Sci. Total Environ. 706, 134430.

Lenhardt, P.P., Brühl, C.A., Berger, G., 2014. Temporal coincidence of amphibian migration and pesticide applications on arable fields in spring. Basic Appl. Ecol. 16, 54–63. https://doi.org/10.1016/j.baae.2014.10.005.

Lenhardt, P.P., Schäfer, R.B., Theissinger, K., Brühl, C.A., 2013. An expert-based landscape permeability model for assessing the impact of agricultural management on amphibian migration. Basic Appl. Ecol. 14, 442–451.

Miaud, C., Sanuy, D., 2005. Terrestrial habitat preferences of the Natterjack toad during and after the breeding season in a landscape of intensive agricultural activity. Amphib. -Reptil. 26, 359–366.

Ockleford, C., Adriaanse, P., Berny, P., Brock, T., Duquesne, S., Grilli, S., Hernandez-Jerez, A.F., Bennekou, S.H., Klein, M., Kuhl, T., Laskowski, R., Machera, K., Pelkonen, O., Pieper, S., Stemmer, M., Sundh, I., Teodorovic, I., Tiktak, A., Topping, C.J., Wolterink, G., Aldrich, A., Berg, C., Ortiz-Santaliestra, M., Weir, S., Streissl, F., Smith, R.H., 2018. Scientific Opinion on the state of the science on pesticide risk assessment for amphibians and reptiles. EFSA J. 16, e05125 https://doi.org/10.2903/j.efsa.2018.5125.

Petrovan, S.O., Schmidt, B.R., 2019. Neglected juveniles; a call for integrating all amphibian life stages in assessments of mitigation success (and how to do it). Biol. Cons. 236, 252–260.

Pradel, R., Hines, J.E., Lebreton, J.D., Nichols, J.D., 1997. Capture-recapture survival models taking account of transients. Biometrics 53, 60–72. https://doi.org/10.2307/2533097.

Pradel, R., Sanz-Aguilar, A., 2012. Modeling trap-awareness and related phenomena in capture-recapture studies. PLoS One 7, e32666.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Relyea, R.A., 2005. The lethal impact of Roundup on aquatic and terrestrial amphibians. Ecol. Appl. 15, 1118–1124.

Renoirt, M., Angelier, F., Cheron, M., Bustamante, P., Cherel, Y., Brischoux, F., 2021. Stable isotopes of a terrestrial amphibian illustrate fertilizer-related nitrogen enrichment of food webs in agricultural habitats. Agr. Ecosyst. Environ. 319, 107553.

Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P., de Carli, E., del Moral, J.C., Domşa, C., Escandell, V., Fontaine, B., Foppen, R., Gregory, R., Harris, S., Herrando, S., Husby, M., Ieronymidou, C., Jiguet, F., Kennedy, J., Klvaňová, A., Kmecl, P., Kuczyński, L., Kurlavičius, P.,

Kålås, J.A., Lehikoinen, A., Lindström, Å., Lorrillière, R., Moshøj, C., Nellis, R., Noble, D., Eskildsen, D.P., Paquet, J.-Y., Pélissié, M., Pladevall, C., Portolou, D., Reif, J., Schmid, H., Seaman, B., Szabo, Z.D., Szép, T., Florenzano, G.T., Teufelbauer, N., Trautmann, S., van Turnhout, C., Vermouzek, Z., Vikstrøm, T., Vořísek, P., Weiserbs, A., Devictor, V., 2023. Farmland practices are driving bird population decline across Europe. Proc. Natl. Acad. Sci. USA 120, e2216573120. https://doi.org/10.1073/pnas.2216573120.

Savic, B., Evgrafova, A., Donmez, C., Vasic, F., Glemnitz, M., Paul, C., 2021. Assessing the role of kettle holes for providing and connecting amphibian habitats in agricultural landscapes. Land 10, 692. https://doi.org/10.3390/land10070692.

Schmidt, B.R., Meier, A., Sutherland, C., Royle, J.A., 2017. Spatial capture-recapture analysis of artificial cover board survey data reveals small scale spatial variation in Slow Worm *Anguis fragilis* density. Roy. Soc. Open Sci. 4, 170374.

Schmidt, B.R., Schaub, M., Anholt, B.R., 2002. Why you should use capture-recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion, and common toads. Amphib. -Reptil. 23, 375–388.

Schwabe, H., 1977. Studien zur potentiellen landwirtschaftlichen Bedeutung der Kreuzkröte *(Bufo calamita* Laur.) im Rhein-Main-Gebiet. Z. F. üR. Angew. Zool. 64, 331–351.

Schwarzkopf, L., Alford, R., 2002. Nomadic movement in tropical toads. Oikos 96, 492–506. https://doi.org/10.1034/j.1600-0706.2002.960311.x.

Schweizer, E., 2016. Resource selection and movement capacity of Natterjack toads (*Epidalea calamita*) in agricultural areas. MSc thesis, Zürcher Hochschule für Angewandte Wissenschaften.

Seufert, V., Ramankutty, N., 2017. Many shades of gray—The context-dependent performance of organic agriculture. Sci. Adv. 3, e1602638.

Siffert, O., Pellet, J., Ramseier, P., Tobler, U., Bergamini, A., Schmidt, B.R., 2022. Where land and water meet: making amphibian breeding sites attractive for amphibians. Diversity 14, 834.

Sinsch, U., 2009. *Bufo calamita* Laurenti, 1768 – Kreuzkröte. In: Grossenbacher, K. (Ed.), Handbuch der Amphibien und Reptilien Europas. Wiebelsheim, Aula-Verlag, pp. 339–413.

Sinsch, U., Oromi, N., Miaud, C., Denton, J., Sanuy, D., 2012. Connectivity of local amphibian populations: modelling the migratory capacity of radio-tracked Natterjack toads. Anim. Conserv. 15, 388–396.

Smalling, K.L., Reeves, R., Muths, E., Vandever, M., Battaglin, W.A., Hladik, M.L., Pierce, C.L., 2015. Pesticide concentrations in frog tissue and wetland habitats in a landscape dominated by agriculture. Sci. Tot. Env. 502, 80–90.

Stevens, V.M., Baguette, M., 2008. Importance of habitat quality and landscape connectivity for the persistence of endangered Natterjack toads. Cons. Biol. 22, 1194–1204.

Stevens, V.M., Polus, E., Wesselingh, R., Schtickzelle, N., Baguette, M., 2004. Quantifying functional connectivity: experimental evidence for patch-specific resistance in the Natterjack toad (*Bufo calamita*). Landsc. Ecol. 19, 829–842.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306, 1783–1786.

Sutherland, C., Munoz, D.J., Miller, D.A.W., Grant, E.H.C., 2016. Spatial capture-recapture: a promising method for analyzing data collected using artificial cover objects. Herpetologica 72, 6–12.

Sutherland, C., Royle, J.A., Linden, D., 2019. oSCR: A Spatial Capture-Recapture R Package for Inference about Spatial Ecological Processes. Ecography 42, 1459–1469.

Swanson, J.E., Muths, E., Pierce, C.L., Dinsmore, S.J., Vandever, M.W., Hladik, M.L., Smalling, K.L., 2018. Exploring the amphibian exposome in an agricultural landscape using telemetry and passive sampling. Sci. Rep. 8, 10045 https://doi.org/10.1038/s41598-018-28132-3.

Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C., Batary, P., 2021. Beyond organic farming – harnessing biodiversity-friendly landscapes. Trends Ecol. Evol. 36, 919–930.

Valdez, J.W., Gould, J., Garnham, J.I., 2021. Global assessment of artificial habitat use by amphibian species. Biol. Cons. 257, 109129 https://doi.org/10.1016/j.biocon.2021.109129.

Wagner, N., Rödder, D., Brühl, C.A., Veith, M., Lenhardt, P.P., Lötters, S., 2014. Evaluating the risk of pesticide exposure for amphibian species listed in Annex II of the European Union Habitats Directive. Biol. Cons. 176, 64–70.

Weltje, L., Simpson, P., Gross, M., Crane, M., Wheeler, J.R., 2013. Comparative acute and chronic sensitivity of fish and amphibians: a critical review of the data. Environ. Toxicol. Chem. 32, 984–994.

Weltje, L., Ufer, A., Hamer, M., Sowig, P., Demmig, P., Dechet, F., 2018. Risk assessment considerations for plant protection products and terrestrial life-stages of amphibians. Sci. Total Environ. 636, 500–511.