The influence of habitat quality on demography, dispersal and population structure of great crested newts (*Triturus cristatus*)

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DEDICATION

I dedicate this dissertation to my wonderful daughters, Smilla and Lilja. Whatever paths in life you may chose and no matter what obstacles or detours you may face, believe in yourself and never lose sight of your goals.

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Abstract

The great crested newt (*Triturus cristatus*) is an amphibian species of European conservation concern that has suffered severe declines, primarily due to habitat loss and fragmentation. This pond-breeding amphibian lives in spatially structured populations (SSPs) where dispersal strongly influences population dynamics, genetics and thereby the long-term persistence of the whole SSP. This dissertation investigates the effects of habitat quality on demography and how such environmental as well as individual factors influence different stages of the dispersal process and consequently the population structure of great crested newts. The evaluation of a commonly used habitat suitability index (HSI) model showed no relationship between habitat quality and individual survival probability or body condition but a positive association with reproduction probability and abundance, making it a useful tool to identify habitats of higher priority for species conservation. A comprehensive analysis of dispersal and population structure combining extensive demographic and genetic data highlights the importance of habitat quality for driving *context-dependent dispersal* and therefore demography and genetic structure in a *patchy population* of great crested newts. Finally, the monitoring of 18 newly created ponds revealed that ponds were rapidly colonized, mostly over short distances, and that newts captured in new ponds were younger and tended to be larger than those in established ponds (*phenotype-dependent dispersal)*, indicating that colonization is predominantly the result of natal dispersal by large individuals. Implications for conservation management are being discussed including corresponding recommendations.

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Angesichts der globalen Biodiversitätskrise stellt der Schutz bedrohter Arten und ihrer Lebensräume eine dringliche Aufgabe unserer Zeit dar. Amphibien gelten als die am stärksten bedrohte Wirbeltierklasse: Sie verzeichnen weltweit besorgniserregende Populationsrückgänge und immer mehr Amphibienarten verschwinden in noch nie dagewesenem Tempo. Dabei gelten die zunehmende Zerstörung, Degradierung und Fragmentierung ihrer Lebensräume als Hauptursachen für das weltweite Amphibiensterben. Amphibien sind ektotherm, besitzen eine durchlässige Haut und die meisten Arten weisen einen komplexen, biphasischen Lebenszyklus auf, der aquatische und terrestrische Entwicklungsstadien beinhaltet, was sie besonders anfällig für Umweltveränderungen macht. Außerdem sind Amphibienpopulationen oft räumlich strukturiert, d.h. dass mehrere Teilpopulationen, die unterschiedliche Fortpflanzungsgewässer besiedeln, durch ab- bzw. einwandernde Individuen miteinander im Austausch stehen. Durch die fortschreitende, von Menschen verursachte Fragmentierung von Amphibien-Lebensräumen werden Teilpopulationen zunehmend isoliert und haben dadurch ein erhöhtes Risiko auszusterben. Die Häufigkeit, die Richtung und die zurückgelegte Distanz individueller Wanderungen haben dabei einen großen Einfluss auf die Dynamik und die genetische Struktur von Amphibienpopulationen und somit letztendlich auch auf deren langfristigen Fortbestand. Ein besseres Verständnis des Wanderverhaltens und des Einflusses der Habitatqualität auf die Dynamik räumlich strukturierter Populationen ist daher von zentraler Bedeutung für das Monitoring, das Management und den Schutz bedrohter Amphibienarten.

Der Nördliche Kammmolch (*Triturus cristatus*) ist in Europa weit verbreitet, verzeichnet aber starke Populationsrückgänge in seinem gesamten Verbreitungsgebiet. Kammmolche werden in den Anhängen II und IV der europäischen FFH-Richtlinie aufgeführt und Mitgliedstaaten sind daher verpflichtet, den Erhaltungszustand dieser Art zu überwachen sowie spezielle Schutzgebiete auszuweisen. Das Monitoring und

Management von Kammmolch-Populationen würde von wissenschaftlich fundierten Methoden und Hilfsmitteln profitieren, mit denen sich die räumliche Verbreitung und die Bestandsentwicklung prognostizieren lassen. Ein umfassendes Verständnis des Wanderverhaltens und der Populationsstruktur ist demzufolge von elementarer Bedeutung für die Entwicklung geeigneter Schutzmaßnahmen und effektiver Managementstrategien für diese bedrohte Amphibienart.

In dieser Dissertation nutze ich Verbreitungs- und Populationsmodelle, um die Eignung eines gängigen Habitatindex für die Prognose der räumlichen Verbreitung und der Populationsdynamik von Kammmolchen zu evaluieren. Darüber hinaus kombiniere ich demographische und genetische Ansätze und integriere ökologische und phänotypische Daten für eine umfassende Analyse des Wanderverhaltens und der Populationsstruktur von Kammmolchen auf lokaler und regionaler Ebene.

Kapitel I – Ein detailliertes Verständnis davon, wie sich die Lebensraumqualität auf die Demographie bedrohter Arten auswirkt, ist von zentraler Bedeutung für die Entwicklung effektiver Schutzmaßnahmen. Habitatmodelle beschreiben funktionale Zusammenhänge zwischen dem Vorkommen oder der Häufigkeit einer Art und verschiedenen Umweltparametern. Sie werden vielfach im Wildtiermanagement und in der Naturschutzpraxis angewendet, um die räumliche Verbreitung von Arten vorherzusagen, Bestandsaufnahmen zu planen oder fundierte Entscheidungen zu ermöglichen. Bei einem gängigen Habitatmodell für den Kammmolch werden zehn biotische und abiotische Schlüsselfaktoren anhand von Expertenwissen bewertet. Anschließend wird ein Habitateignungsindex (HSI) berechnet, welcher die Qualität eines Gewässers als Lebensraum für diese Art quantifiziert. Der HSI wird auf einer Skala von 0 bis 1 abgebildet, wobei höhere Werte eine bessere Eignung anzeigen. Der HSI für den Kammmolch wurde ursprünglich für den Gebrauch in Großbritannien entwickelt und mit Hilfe eines Populationsindex validiert. Dabei wurde eine positive Korrelation zwischen dem HSI und der Anzahl an gefangenen oder gesichteten Individuen in einem Gewässer festgestellt. Solche Populationsindizes berücksichtigen allerdings nicht das Problem der unvollständigen Bestandserfassung (*imperfect detection*), was zu einer verzerrten Einschätzung der Art-Habitat-Beziehung führen könnte. Zur Validierung des HSI haben wir die räumliche Übertragbarkeit des Modells überprüft und untersucht, ob sich mit seiner Hilfe Kammmolch-Vorkommen innerhalb eines Untersuchungsgebiets in Deutschland ermitteln lassen. Dabei haben wir

Verbreitungsmodelle (*occupancy models*) genutzt, um das Problem der unvollständigen Bestandserfassung zu berücksichtigen. Um die Auswirkungen der Habitatqualität auf demographische Prozesse besser zu verstehen, haben wir außerdem den Zusammenhang zwischen dem HSI und der Überlebens- und der Fortpflanzungswahrscheinlichkeit von Kammmolchen analysiert.

In unserem Untersuchungsgebiet konnte der HSI das Vorkommen von Kammmolch-Populationen in den verschiedenen Gewässern nicht zuverlässig vorhersagen und stand auch in keinem Zusammenhang zur Überlebenswahrscheinlichkeit der Individuen. Allerdings stieg die Wahrscheinlichkeit, dass sich Kammmolche in einem Gewässer erfolgreich fortpflanzten, mit zunehmenden HSI-Werten an. Folglich könnte der HSI in der Naturschutzpraxis verwendet werden, um Gewässer zu identifizieren, die für den Schutz der Gesamtpopulation von höherer Priorität sind, da sie reproduzierende Populationen beherbergen. Auf diese Weise kann der HSI ein wertvolles Hilfsmittel für die Planung von zielgerichteten Schutzmaßnahmen für Kammmolche darstellen.

<u>*Kapitel II*</u> – Bei der Verwendung von Habitatmodellen in der Naturschutzpraxis wird oftmals angenommen, dass besser geeignete Habitate häufiger von einer Art genutzt werden und dass die dort lebenden Individuen auf Grund der positiven Lebensbedingungen auch eine bessere körperliche Verfassung haben. Dies hätte zur Folge, dass Populationen dort länger überdauern könnten. Allerdings müssen Indices, welche die Eignung eines Habitats für das Vorkommen einer Art anzeigen, nicht notwendigerweise auch Rückschlüsse über den Zustand der dort lebenden Individuen oder Populationen zulassen. Wir haben den Zusammenhang zwischen dem HSI und der Anzahl sowie der körperlichen Konstitution (*body condition* – gemessen mit Hilfe von drei unterschiedlichen Indices) von Kammmolchen in 23 Gewässern einer räumlich strukturierten Population analysiert.

In Gewässern mit besserer Habitatqualität (gemessen mittels HSI) konnten mehr Kammmolche nachgewiesen werden. Allerdings fanden wir keinen Zusammenhang zwischen dem HSI und der körperlichen Konstitution der Molche in den verschiedenen Gewässern. Wir konnten aber zeigen, dass sich diese mit zunehmender Populationsgröße verschlechterte, was vermutlich auf einen dichteabhängigen Anstieg der innerartlichen Konkurrenz zurückzuführen ist. Da eine schlechtere körperliche Konstitution bei Amphibien zu einer Verminderung der Fruchtbarkeit führen kann, könnte dies einen regulierenden Mechanismus in der Populationsdynamik von Molchen darstellen.

Kapitel III – Da Kammmolche für ihre Fortpflanzung an Gewässer gebunden sind, welche unregelmäßig in der Landschaft verteilt vorkommen, bilden sich oftmals räumlich strukturierte Populationen (*spatially structured populations*, *SSPs*). Bei SSPs stehen mehrere Teilpopulationen aus verschiedenen Fortpflanzungsgewässern durch ab- bzw. einwandernde Individuen miteinander im Austausch. Dabei haben die Häufigkeit und die Richtung individueller Wanderungen einen maßgeblichen Einfluss auf die Demographie und die genetische Struktur der Gesamtpopulation. Diese Parameter werden daher genutzt, um verschiedene Varianten von SSPs zu unterscheiden (z.B. *Levins-type metapopulation*, *patchy population, source-sink system*). Um das Wanderverhalten und die Populationsstruktur von Kammmolchen detailliert zu untersuchen, haben wir eine umfangreiche Fang-Wiederfang-Studie durchgeführt und diese mit umfassenden genetischen Analysen kombiniert. Dabei haben wir die Fanghistorien von insgesamt 5564 Individuen in 27 Gewässern ausgewertet und 950 dieser Individuen zusätzlich mit Hilfe von 17 Mikrosatelliten genotypisiert. Außerdem haben wir analysiert, welchen Einfluss die Habitatqualität auf die Immigration, die Emigration, das Überleben und die Reproduktion von Kammmolchen hat. Um die genetische Struktur und den Genfluss auf regionaler Ebene besser zu verstehen, haben wir darüber hinaus noch genetische Daten aus sechs weiteren Gebieten in die Untersuchung mit einbezogen.

Sowohl die demographischen, als auch die genetischen Untersuchungen haben gezeigt, dass Wanderungen zwischen den Gewässern der SSP häufig waren. Die untersuchte SSP zeigte somit die Charakteristika einer *patchy population*, d.h. die Subpopulationen in den einzelnen Gewässern standen untereinander in enger Wechselbeziehung. Dabei legten die Gewässerwechsler zumeist nur kurze Distanzen (≤ 400 m) zurück, obwohl wir auch einige wenige Fälle von Langstreckenwanderung (> 1 km) beobachten konnten. Das Wanderverhalten der Kammmolche war kontextabhängig: Während sich die Habitatqualität (gemessen mittels HSI) nur geringfügig auf die Abwanderung von Individuen aus einem Gewässer auswirkte, konnten wir zeigen, dass Molche bevorzugt in Gewässer mit guter Habitatqualität einwanderten. Die Überlebenswahrscheinlichkeiten von Kammmolchen in guten und in schlechten Gewässern unterschieden sich nicht voneinander, wohingegen die

Fortpflanzungswahrscheinlichkeit mit zunehmender Habitatqualität anstieg. Daher legen unsere Ergebnisse nahe, dass die Gewässerwahl der Molche nicht auf einer Strategie zur Maximierung der Überlebenswahrscheinlichkeit basierte, sondern vielmehr auf einer Optimierung des Fortpflanzungserfolgs. Die hohen Wanderraten innerhalb der SSP führten zu einem hohen Genfluss zwischen den Gewässern, was eine geringe Verwandtschaft der Molche innerhalb der Gewässer sowie eine schwache genetische Differenzierung auf lokaler Ebene zur Folge hatte. Auf regionaler Ebene fanden wir dagegen eine signifikante und hierarchische genetische Differenzierung sowie wenig Wanderung zwischen den Untersuchungsgebieten, was auf das Vorhandensein mehrerer voneinander unabhängiger Populationen schließen lässt.

Kapitel IV – Angesichts der zunehmenden Beeinträchtigung und Zerstörung von Kleingewässern und der fortschreitenden Fragmentierung von Landschaften gilt die Neuanlage von Teichen als wichtige Schutzmaßnahme für bedrohte Amphibienarten. Doch wie effektiv sind solche Maßnahmen und welche Faktoren beeinflussen den Besiedlungsprozess neuer Teiche? Phänotypische Merkmale (z.B. Größe, körperliche Konstitution) können das Wanderverhalten von Individuen beeinflussen (*phenotype-dependent dispersal*) und könnten somit auch eine entscheidende Rolle für die erfolgreiche Besiedelung neuer Habitate spielen. Die phänotypischen Merkmale von Individuen in neuen Gewässern könnten sich daher von denen in älteren Gewässern unterscheiden. Wir haben den Besiedlungsprozess von 18 neu angelegten Teichen, die zeitgleich in ein bestehendes Gewässer-Netzwerk einer räumlich strukturierten Kammmolch-Population integriert worden sind, über einen Zeitraum von drei Jahren beobachtet. Mit Hilfe einer Fang-Wiederfang-Studie sowie genetischen und phänotypischen Daten haben wir das räumlich-zeitliche Besiedlungsmuster analysiert, zurückgelegte Wanderdistanzen von Individuen in den neuen Teichen ermittelt und phänotypische Merkmale (Größe, körperliche Konstitution und Alter) von männlichen und weiblichen Kammmolchen in neuen und älteren Teichen miteinander verglichen.

Die neu angelegten Teiche wurden rasch besiedelt und in etwa der Hälfte der neuen Gewässer, in denen adulte Molche gefangen wurden, konnten wir auch Larven nachweisen. Obwohl die Kammmolche, die in den neuen Teichen gefangen wurden, aus nahe gelegenen älteren Gewässern stammten, zeigte sich, dass diese Tiere meist nicht in den räumlich nächstgelegenen neuen Teich eingewandert waren. Vielmehr legen unsere Beobachtungen nahe, dass die Molche bevorzugt in solche Gewässer einwanderten, die einen höheren Fortpflanzungserfolg versprachen (*context-dependent dispersal*). Außerdem haben unsere Untersuchungen gezeigt, dass Individuen in neuen Teichen jünger und tendenziell größer waren, als solche in älteren Gewässern (*phenotype-dependent dispersal*). Die Besiedelung neuer Teiche scheint somit in erster Linie durch große Individuen zu erfolgen, die von ihrem Geburtsort abwandern (*natal dispersal*). Während die Weibchen in den neuen Teichen eine bessere körperliche Konstitution hatten, als solche in älteren Gewässern, konnten wir bei Männchen das Gegenteil beobachten. Dies lässt auf geschlechtsspezifische Unterschiede im Wanderverhalten schließen.

Zusammengenommen verdeutlichen die Ergebnisse der vorliegenden Dissertation den Einfluss der Habitatqualität auf die Demographie, das Wanderverhalten und die Populationsstruktur von Amphibien. Die Habitatqualität (gemessen mittels HSI) beeinflusst das Vorkommen, die Häufigkeit, aber auch den Fortpflanzungserfolg und das Wanderverhalten von Kammmolchen. Daher ist die Wiederherstellung oder Verbesserung der Habitatqualität von außerordentlicher Bedeutung für den erfolgreichen Schutz bedrohter Kammmolch-Populationen. Mögliche Schutz- und Pflegemaßnahmen beinhalten die Entfernung von Fischen und Uferbeschattung bei bestehenden Gewässern sowie die Neuanlage von Teichen in deren Nähe. Letztere können auch als Trittsteinbiotope (*stepping stones*) fungieren und somit Langstreckenwanderungen erleichtern, was im Idealfall zu einem funktionierendem Habitat-Netzwerk und zu lebensfähigen *patchy populations* führen kann.

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Dissertation

In light of the current global biodiversity crisis, the conservation of threatened species and habitats is a critical issue of our time. Amphibians are recognized as the most threatened vertebrate class, suffering from severe population declines and species extinctions at unprecedented rates. Habitat loss, degradation, and fragmentation are considered the leading causes of amphibian population declines worldwide. Amphibians are ectotherms with highly permeable skin and a complex biphasic life cycle (including aquatic and terrestrial stages), making them particularly vulnerable to environmental changes. Moreover, they often live in spatially structured populations (SSPs), where local populations occupy discrete aquatic breeding patches that are interconnected by dispersing individuals. As landscapes become increasingly fragmented due to human activities, local populations become more isolated and consequently more prone to extinction. Dispersal rates, directions and covered distances strongly influence population dynamics and genetics, and ultimately the long-term persistence of amphibian SSPs. Understanding dispersal patterns and elucidating the role of habitat quality in shaping wildlife population dynamics is therefore central to the monitoring, management and recovery of threatened amphibian species.

The great crested newt (*Triturus cristatus*) is a pond-breeding amphibian of European conservation concern. Although widespread in Europe, this species has suffered severe declines throughout the distribution range. *T. cristatus* is listed in Annexes II and IV of the European Habitats Directive (92/43/EEC) and member states are therefore required to monitor its conservation status and to designate special areas of conservation for this species. Monitoring and management of great crested newt populations would benefit from scientifically substantiated methods and tools for predicting the spatial distribution, abundance, and demography of this species. A profound understanding of dispersal and population structure is crucial for the development of appropriate conservation measures and effective management strategies for this threatened amphibian species.

In this dissertation, I use occupancy and capture-recapture modelling to evaluate the practical applicability of a commonly used habitat suitability index for the prediction of species distribution and population dynamics of great crested newts. Moreover, I combine demographic and genetic approaches and integrate environmental and phenotypic data to provide a comprehensive analysis of dispersal and population structure on local and regional scales.

Chapter I – Elucidating the relationship between habitat quality and demography is critical for the effective conservation of threatened species. Habitat suitability models correlate species occurrence or abundance records with environmental variables. They are broadly applied in wildlife management and conservation practice to predict species distributions, to develop biological surveys, and to guide decision-making processes. A commonly used habitat suitability model for the great crested newt incorporates the evaluation of ten biotic and abiotic key factors using expert opinion. The output of this model is a habitat suitability index (HSI) that indicates the potential quality of a pond for great crested newts, ranging from 0 (representing unsuitable habitat) to 1 (representing optimal habitat). The HSI was originally designed for use in Great Britain and was validated using an index of abundance. The authors found a positive relationship between the HSI and the maximum number of newts caught or counted on a single occasion. However, abundance indices ignore the problem of imperfect detection, probably leading to biased estimates of species-habitat relationships. In order to validate the HSI, we assessed its transferability by testing its capacity to predict the spatial distribution of great crested newts in a study area in Germany using occupancy modelling to account for imperfect detection. Furthermore, we analysed the relationship between the HSI and reproduction and survival probabilities of great crested newts to provide a better understanding of the effects of habitat quality on demographic processes shaping population dynamics.

In our study area, the HSI did not predict species occurrence reliably and was also not related to survival probabilities of great crested newts. However, we showed that successful breeding was more likely to occur in ponds with higher HSI values. If the HSI indicates breeding populations rather than mere species occurrence, conservation managers may utilize it to identify habitats of higher priority for species conservation

(i.e. ponds harbouring healthy populations). The HSI may therefore constitute a valuable tool for guiding targeted conservation measures for great crested newts.

<u>*Chapter II*</u> – In the application of HSI models for management purposes, it is often assumed that habitat suitability predicts species performance (i.e. individuals fare better and are more abundant in suitable habitat patches than in unsuitable patches) and consequently population persistence. However, indices of habitat suitability may not always correlate with individual or population state variables relevant for population persistence. We studied the relationship between the HSI and parameters describing species performance at the level of individuals (i.e. body condition measured using three different indices) and of populations (i.e. population size) using capture-recapture data from 23 ponds harbouring a large SSP of great crested newts.

Ponds of higher suitability (as defined by the HSI) harboured larger populations. We did not find a relationship between the HSI and body condition of great crested newts. However, population size correlated negatively with body condition of individuals, possibly due to an increased intraspecific competition for resources. Since lower body condition may lead to reduced fecundity in amphibians, we suggest that a population-size dependent reduction of body condition may be a regulatory mechanism in the dynamics of newt populations.

<u>*Chapter III*</u> – Great crested newts depend on aquatic habitats for reproduction that are patchily distributed across the landscape, leading to the emergence of spatially structured populations (SSPs). SSPs are composed of a set of breeding populations occupying discrete habitat patches that are interconnected by dispersing individuals. Dispersal rates and directions have a strong impact on the demography and the genetic structure of SSPs and are therefore important for the classification of different types of SSPs (i.e. *Levins-type metapopulation*, *patchy population,* and *source-sink system*). For a comprehensive analysis of dispersal patterns and population structure of great crested newts, we studied a large SSP using an extensive mark-recapture and a powerful genetic dataset. We analysed the capture-recapture data of 5564 marked individuals in 27 ponds and genotyped 950 individuals for 17 microsatellite loci. Furthermore, we evaluated the influence of habitat quality on immigration, emigration, survival, and reproduction probabilities. In order to assess genetic structure and gene flow at a regional level, we added genetic data from six sampling sites outside the SSP.

Both, demographic and genetic analyses indicated high dispersal rates between ponds at the level of the SSP. The studied SSP thus behaved like a *patchy population* where local breeding populations were demographically interdependent. The mark-recapture study revealed that dispersal distances were predominantly short (≤ 400 m), even though we detected a few rare events of long-distance dispersal (> 1 km). Dispersal was *context-dependent*: Although habitat quality (as defined by the HSI) marginally affected emigration probability, it strongly influenced immigration probability (i.e. individuals preferentially immigrated into high quality ponds). While survival probability did not differ between high-quality and low-quality ponds, reproduction probability increased with increasing habitat quality. Hence, our results suggest that adult pond choice did not result from a strategy to maximize survival but rather to maximize reproductive success. High dispersal rates led to intense gene flow and consequently to low relatedness of individuals within ponds and to a weak genetic structure on the level of the SSP. At the regional level, however, a strong hierarchical genetic structure with very few first-generation migrants as well as low effective dispersal rates suggested the presence of several independent demographic units.

Chapter IV – In order to compensate for the ongoing degradation and loss of aquatic breeding habitats and to facilitate long-distance dispersal in fragmented landscapes, conservation efforts for pond-breeding amphibians often include the creation of new ponds. Evaluating the effectiveness of such conservation measures and investigating factors influencing the colonization process of newly created ponds may advance conservation practice substantially. Phenotypic traits (e.g. body size, body condition) can affect individual dispersal decisions (leading to *phenotype-dependent dispersal*) and may also be important drivers of colonization success. Hence, the phenotypic composition of populations in recently colonized habitat patches may differ from that of populations occurring in established habitats. We monitored the colonization process of 18 newly created ponds that were concurrently integrated in a network of 33 established ponds harbouring an extensive SSP of great crested newts. We combined mark-recapture, genetic, and phenotypic data to analyse the spatiotemporal pattern of colonization during the first three years after pond construction, determined dispersal distances of colonizers, and compared phenotypic traits (i.e. body size, body condition, and age) of males and females captured in new and established ponds.

New ponds were rapidly colonized and successful breeding was observed in half of the occupied ponds. Although most colonizers dispersed to new ponds located in the proximity of their source pond, the majority was not found in the closest new pond. Instead, our observations support the assumption that great crested newts adjust their dispersal decisions according to environmental cues that reflect the fitness prospects of a patch, resulting in *context-dependent dispersal*. Moreover, we found evidence for *phenotype-dependent dispersal*: newts captured in new ponds were younger and tended to be larger than those in established ponds, indicating that colonization is mostly the result of *natal dispersal* by large individuals. While females in new ponds had higher body condition than those in established ponds, the opposite was true for male great crested newts, indicating sex differences in dispersal strategies.

Overall, the results of this dissertation highlight the influence of habitat quality on demography, dispersal and population structure of pond-breeding amphibians. Habitat quality (as defined by the HSI) influences the occurrence, abundance, but also reproductive success and dispersal of great crested newts. Hence, restoring and improving habitat quality are key to successful conservation of threatened great crested newt populations. Conservation efforts should include the removal of predatory fish or shading trees, as well as the creation of new ponds in proximity to existing ones. These may also function as stepping stones to facilitate dispersal over longer distances, ideally leading to a functional habitat network and viable *patchy populations*.

Introduction

The pace of biodiversity loss and ecosystem degradation is advancing at an alarming rate (IPBES, 2019), making the conservation of threatened species and habitats a critical issue of our time. Amphibians are the most endangered vertebrate class, suffering from severe population declines and species extinctions at unprecedented rates (Stuart et al., 2004). More than 40 percent of amphibian species are at risk of extinction (IPBES, 2019). Pollution, global climate change, over-exploitation, and alien invasive species and pathogens (e.g. *Batrachochytrium dendrobatidis* and *B. salamandrivorans*) are key drivers behind this trend (Blaustein et al., 2011). However, habitat loss, degradation, and fragmentation are the major contributing factors to amphibian population declines worldwide (Chanson *et al.*, 2008).

Habitat quality and availability have fundamental effects on amphibian diversity and distribution. Amphibians are ectotherms with a highly permeable skin, making them particularly susceptible to environmental changes (Hopkins, 2007). Moreover, most amphibians exhibit complex biphasic lifecycles with an aquatic larval stage followed by metamorphosis into a more terrestrial adult form. Accordingly, amphibians require both, suitable aquatic habitat for reproduction and larval development as well as diverse surrounding terrestrial habitat for hibernation, migration, foraging, and dispersal (Semlitsch, 2008). Pond-breeding amphibians often live in spatially structured populations (SSPs) where local populations occupy discrete aquatic breeding patches (i.e. ponds or ditches) that are connected by dispersing individuals (Cayuela et al., 2018). Dispersal strongly influences the spatial dynamics of such population networks as well as their ability to cope with habitat degradation and fragmentation (Cayuela et al., 2018; Arntzen et al., 2017).

Dispersal describes the unidirectional movement of an individual from its natal patch to its first breeding patch (*natal dispersal*) or between successive breeding patches (*breeding dispersal*). The process of dispersal can be divided into three stages: emigration from a habitat patch, transience in the landscape matrix, and immigration into a new habitat patch (Ronce, 2007). All of these stages can be influenced by the internal state of individuals (e.g. morphology, physiology, behaviour), resulting in *phenotype-dependent dispersal*, as well as by external information (i.e. social factors and/or environmental conditions), leading to *context-dependent dispersal*. Both, *phenotype-* and *context-dependent dispersal* have far-reaching consequences for the demography and the genetic structure of amphibian SSPs and thus for their effective conservation (Cayuela et al., 2018).

In Europe, amphibian habitats are affected by multiple stressors, most of which are directly or indirectly related to human activities. Drainage, infilling, land-use conversion, mismanagement as well as increased agricultural, urban, and industrial runoff are putting freshwater ecosystems under strong pressure (Temple & Cox, 2009). Agricultural expansion and intensification, urbanization and the associated construction of linear transport infrastructure contribute to the fragmentation of terrestrial habitats, leading to the disruption of seasonal migration pathways and the impediment of dispersal (Cushman, 2006; Arntzen et al., 2017). As landscapes become increasingly fragmented, reduced patch size and interpatch dispersal result in smaller effective population sizes within remaining suitable habitat patches with a variety of demographic and genetic consequences (Cheptou et al., 2017): At the demographic level, small populations are more prone to extinction due to stochastic effects (e.g. random fluctuations in birth rate, death rate, sex ratios; environmental variability). At the genetic level, small isolated populations experience increased levels of inbreeding and a greater impact of genetic drift, resulting in the erosion of genetic diversity and a reduced capacity to adapt to environmental change. In the face of ongoing anthropogenic habitat alteration and fragmentation, a profound understanding of species-habitat relationships, dispersal patterns, and population structure is crucial for the management of natural populations and the development of effective conservation strategies for threatened amphibian species.

The great crested newt (*Triturus cristatus*)

The great crested newt (*Triturus cristatus*), also known as northern crested newt, is an important European flagship species for amphibian conservation (O'Brien et al., 2014). Adults can reach up to 20 cm in total body length, with females being typically larger than males, and can live for up to 16 years in the wild (Miaud et al., 1993). The skin of this pond-breeding amphibian is granular in appearance and the body is generally dark brown to black in colour, while the belly is bright yellow or orange with an irregular pattern of dark spots. The ventral colour pattern is highly variable and can be used for individual identification, similar to a human fingerprint (Hagström, 1973). During the breeding season, males develop a conspicuous, jagged crest along their back (Jehle et al., 2011), giving them a dragon-like appearance (Figure 1).

Figure 1: Male great crested newts (*Triturus cristatus*) develop a jagged dorsal crest during the breeding season. © Burkhard Thiesmeier, Laurenti-Verlag.

Great crested newts are widespread across northern and central Europe and can also be found in parts of Western Siberia. However, populations have suffered severe declines throughout the distribution range (Edgar & Bird, 2006; Denoël, 2012). These charismatic amphibians have more demanding habitat requirements than most other palaearctic newt species (Arntzen & Teunis, 1993) and as a result, have declined more severely. *T. cristatus* is listed in Annexes II and IV of the European Habitats Directive (92/43/EEC). EU member states are therefore required to monitor the conservation status of this species and to designate special areas of conservation which must be managed in accordance to the ecological requirements of great crested newts.

In this dissertation, I use occupancy and capture-recapture modelling to assess whether a commonly used habitat suitability model for great crested newts predicts the spatial distribution of this threatened amphibian as well as demographic processes affecting population dynamics (i.e. reproduction, survival, immigration, and emigration) and species performance (i.e. population size and body condition of individuals). Furthermore, I combine demographic, genetic, phenotypic, and ecological data to reveal internal and external determinants of dispersal, and its consequences for population structure. Finally, I study the colonization process of 18 newly created ponds in order to evaluate the effectiveness of this conservation tool for *T. cristatus*.

Habitat Suitability Models

Understanding the relationship between habitat quality and demography is crucial for the monitoring, management and recovery of threatened species. Habitat suitability models (also known as species distribution models or ecological niche models) relate species occurrence or abundance records with environmental variables. These models provide useful information on the ecological requirements of a target species and can be used to predict species distribution across space and time (Elith & Leathwick, 2009). Habitat suitability models are broadly applied in wildlife management and conservation practice to develop biological surveys, to assess management priorities, and to guide decision-making processes (Zajac, et al. 2015). A commonly used habitat suitability model for the great crested newt was developed by Oldham et al. (2000) and incorporates the evaluation of ten suitability indices (SI), all of which are considered to influence the presence and abundance of this species (Table 1). The habitat suitability index (HSI) is then calculated as geometric mean of these ten variables and indicates the potential quality of a pond for great crested newts, ranging from 0 (representing unsuitable habitat) to 1 (representing optimal habitat).

The HSI for great crested newts was originally designed for use in Great Britain and was validated using an index of abundance. However, abundance indices ignore the problem of imperfect detection (i.e. individuals or populations are not always detected even when present), which may lead to biased estimates of species-habitat relationships (Anderson, 2001). In **Chapter I**, we evaluated the spatial transferability of the HSI using occupancy modelling to account for imperfect detection. To better understand how great crested newts respond to variation in habitat quality, we studied the relationship between the HSI and demographic processes shaping population dynamics (i.e. reproduction and survival probabilities).

Table 1: Ten Suitability Indices (SI) for the calculation of the Habitat Suitability Index (HSI) for *Triturus cristatus* (according to Oldham et al., 2000).

SI	Factor	Operationalisation of SI value	Optimal for *T. cristatus*
SI_1	Location	3-point scale based upon map (Zone A, B, C; only Great Britain)	Zone A
SI_2	Pond area	Pond surface area (m²)	500-700 m²
SI_3	Pond drying	Frequency of desiccations per decade	One desiccation in 10 years
SI_4	Water quality	4-point scale based on invertebrate community as indicators of pollution	Diverse invertebrate community
SI_5	Shade	Percentage of perimeter shaded	0-60 %
SI_6	Fowl	Number of waterfowl per pond or per 1000m² in large ponds	Maximum one pair of waterfowl
SI_7	Fish	4-point scale based on fish presence/abundance	Absent
SI_8	Pond count	Number of ponds within 1km of the survey pond	≥4 ponds per km²
SI_9	Terrestrial habitat	"Newt-friendly" habitat (e.g. forests, meadows, hedges, ditches) within a radius of 500m	≥4 ha of "newt-friendly" habitat without serious barriers
SI_{10}	Macrophyte cover	Percentage of pond surface covered by macrophytes	70-80 %

In the application of habitat suitability models for management purposes, it is often assumed that habitat suitability predicts species performance (Thuiller et al., 2010; Lee-Yaw et al., 2021). In other words, that individuals fare better and are more abundant in habitat patches that are more suitable for the species, resulting in a higher probability of population persistence. The range of environmental conditions that allow a species to occur and to persist in a habitat patch describes its ecological niche (Schoener, 2009). The ecological niche is frequently quantified using habitat suitability models (Guisan & Thuiller, 2005). However, habitat suitability based on the modelled relationship between occurrence records and the environment may not always correlate with individual or population state variables relevant for population persistence (Guisan et al., 2013; Bean et al., 2014). This might be due to the fact that individuals can be found in unsuitable habitat patches (e.g. in source-sink systems;

Pulliam, 1988) or species may be absent from suitable habitat patches (e.g. in metapopulations; Hanski, 1998). In **Chapter II**, we evaluated the predictive power of the HSI for parameters describing species performance at the level of individuals (i.e. body condition) and of populations (i.e. population size).

Dispersal and population structure

Great crested newts depend on aquatic habitats (e.g. ponds or ditches) for reproduction, which can be quite numerously and patchily distributed across the landscape, leading to the emergence of spatially structured populations (SSPs). SSPs are composed of a set of breeding ponds that are regulated by local demographic processes (i.e. mortality and natality) and that are interconnected by dispersing individuals (via immigration and emigration; Thomas & Kunin, 1999). Dispersal rates, directions, and covered distances strongly influence the demography, the genetic structure, and ultimately the long-term persistence of the whole SSP (Hanski & Gaggiotti, 2004).

Therefore, dispersal is tremendously important for the classification of different types of SSPs (i.e. *Levins-type metapopulation*, *patchy population,* and *source-sink system*). 1. Dispersal rates determine the position of an SSP along a gradient from *Levins-type metapopulation* to *patchy population* (Ovaskainen & Hanski, 2004). At one end of the gradient, an SSP shows the characteristics of the classic *Levins-type metapopulation* (Levins, 1969), where most individuals remain in their natal patch and dispersal rates between subpopulations are rare but sufficiently high to allow the recolonization of patches where a subpopulation has gone extinct. At the other end of the gradient, an SSP can behave as a *patchy population* (Harrison, 1991), where individuals disperse frequently among patches and reproduce in several patches during their lifetime so that the network forms a single demographic unit which is unlikely to go extinct. 2. The directional asymmetry of dispersal is another aspect for the classification of SSPs. In *source-sink systems*, individuals from productive high-quality patches (i.e. *sources*) move to low-quality patches (i.e. *sinks*), where local reproductive success fails to balance local mortality, thereby allowing the long-term persistence of subpopulations in low-quality habitats (Pulliam, 1988). However, if individuals adjust their dispersal decisions according to social and/or environmental cues (i.e. “informed dispersal” *sensu* Clobert et al., 2009), they should preferentially immigrate to high-quality patches, where local fitness prospects are higher, resulting in *context-dependent dispersal*. In **Chapter III**, we provide a comprehensive analysis of dispersal and population structure of great crested newts. Based on an extensive mark-recapture dataset (5564 marked individuals in 27 ponds) and a powerful genetic dataset (1266 individuals genotyped for 17 microsatellite loci), we assessed whether the studied SSP behaves like a *Levins-type metapopulation*, a *patchy population* or a *source-sink system*. Moreover, we evaluated the influence of habitat quality on survival and reproduction probabilities as well as on immigration and emigration probabilities. Finally, we assessed genetic structure and gene flow at a regional level (~350km²) by adding genetic data from six sampling sites outside the SSP.

Pond creations

Great crested newts prefer diverse terrestrial habitats that contain a variety of nearby ponds used for breeding and larval development (Edgar & Bird, 2006). Ponds also act as stepping-stones facilitating dispersal, thereby increasing population connectivity in the landscape (Semlitsch, 2000). Despite their significant contribution to ecosystem services (e.g. water supply, nutrient retention, carbon cycling) and to biodiversity (Biggs et al., 2017), freshwater habitats are among the most endangered habitat types in Europe (Temple & Cox, 2009). Major threats include increased nutrient loading, pollution, mismanagement, fish stocking, land drainage, and infilling (Brönmark & Hansson, 2017). In order to compensate for the ongoing degradation and loss of aquatic breeding habitats and to sustain viable populations, conservation efforts for pond-breeding amphibian species often include the restoration and creation of ponds (Baker & Halliday, 1999). Studying the effectiveness of such conservation actions and identifying factors influencing the colonization process hold the potential to advance conservation practice substantially (Schmidt et al., 2019).

Colonization can be defined as a process whereby individuals disperse to and become established in suitable but currently unoccupied habitats. Phenotypic traits (e.g. morphology, physiology, behaviour) can influence each step of the dispersal process, leading to *phenotype-dependent dispersal* and *dispersal syndromes* (Clobert et al., 2009). Phenotypic traits may also be important drivers of colonization success and the phenotypic composition of populations in recently colonized habitat patches may therefore differ from that of populations occurring in established habitat patches (Clobert et al., 2009). In **Chapter IV**, we used mark-recapture, genetic, and phenotypic data to analyse the colonization process of 18 ponds concurrently created to support an existing pond network harbouring a large SSP of great crested newts. We analysed the spatiotemporal pattern of colonization during the first three years after pond construction, determined dispersal distances covered by colonizers, and discussed possible implications for conservation management. Furthermore, we compared phenotypic traits related to dispersal (i.e. body size, body condition, and age) of males and females captured in new and established ponds.

Figure 2: Four out of 18 newly created ponds. Photographed three years after construction. © Bianca Unglaub

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Chapter I

Linking habitat suitability to demography in a pond-breeding amphibian

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Linking habitat suitability to demography in a pond-breeding amphibian

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Abstract

Introduction: Elucidating the relationship between habitat characteristics and population parameters is critical for effective conservation. Habitat suitability index (HSI) models are often used in wildlife management and conservation practice assuming that they predict species occurrence, abundance and demography. However, the relationship between vital rates such as survival and reproduction and habitat suitability has rarely been evaluated. In this study, we used pond occupancy and mark-recapture data to test whether HSI predicts occupancy, reproduction and survival probabilities. Our model species is the great crested newt (*Triturus cristatus*), a pond-breeding amphibian protected under the European Habitats Directive.

Results: Our results show a positive relationship between the HSI and reproduction probability, whereas pond occupancy and survival probabilities were not related to HSI. Mortality was found to be higher during breeding seasons when newts are in ponds than during terrestrial phases of adult newts.

Conclusion: Habitat suitability models are increasingly applied to wildlife management and conservation practice. We found that the HSI model predicted reproduction probability, rather than occurrence or survival. If HSI models indicate breeding populations rather than mere species occurrences, they may be used to identify habitats of higher priority for conservation. Future HSI models might be improved through modelling breeding populations vs. non-breeding populations rather than presence/absence data. However, according to our results the most suitable habitat is not necessarily the habitat where demographic performance is best. We recommend that conservation practitioners should use HSI models cautiously because there may be no direct link between habitat suitability, demography and consequently, population viability.

Keywords: Environmental niche model, Habitat suitability index (HSI), Species distribution, Reproduction probability, Survival probability, *Triturus cristatus*

Introduction

Understanding the relationship between habitat quality and demography is central to the monitoring, management and recovery of threatened species. Species distribution models, also known as ecological niche models or habitat suitability models, relate species occurrence data to environmental variables. These models provide useful information on the ecological requirements of species and are widely used to predict species distribution, making them valuable tools for habitat management, impact assessment and conservation practice [1-3].

For practical application and habitat suitability assessments in the field, the output of statistical species distribution models has often been simplified to habitat suitability indices (HSI). These indices are based on habitat characteristics that can easily be measured in the field or derived from digital maps [4]. A HSI is a numerical index, ranging from 0 (unsuitable habitat) to 1 (optimal habitat). In the application of HSI models for management purposes, it is often assumed that habitat suitability predicts species performance and demography [5]. However, the most suitable habitat or habitats where density is high do not necessarily constitute habitats where demographic performance is best [6,7]. Moreover, despite being important for the management of threatened

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species, whether habitat suitability is associated with species occurrence [8-12] and demographic parameters, e.g. reproductive success [5,13,14] and apparent survival [15,16], has rarely been evaluated. Such tests are important because several studies did not find the expected link between habitat suitability and species occurrence or demography [9,11,17]. Species may not occur in suitable patches when structured as a metapopulation [18] or they may be found in unsuitable patches (i.e. so called sinks, [19]). To predict how species may respond to variation in habitat quality, it is necessary to understand the demographic processes through which the environment influences distributions and population dynamics [19-21]. Hence, vital rates can potentially be informative when validating HSI models [22].

In this study, we contribute to the validation of simple and easily applicable HSI models as predictive tools for management purposes. We studied the relationship between a commonly used HSI [23] and occurrence/demographic parameters in the great crested newt (*Triturus cristatus*). While a positive relationship between the HSI and newt abundance was reported [23], this assessment of the HSI is problematic as abundance is not necessarily a good indicator of habitat quality and abundance indices ignore imperfect detection [6,24]. Evidence for a relationship between HSI and newt abundance or newt occurrence is mixed. While there was no relationship between abundance indices and HSI in [25], a study on great crested newt pond occupancy that accounted for imperfect detection found that HSI predicted newt occurrence [12]. However, HSI values differed only slightly between ponds with and without newts (mean HSI ± SD: 0.70 ± 0.12 and 0.61 ± 0.13, respectively [12]). Here, we used three variables that are often used to describe the state of animal populations: species occurrence, occurrence of reproduction and survival. At the phenomenological level, we tested whether the simple HSI for great crested newts, which is based on only ten habitat characteristics, predicts species occurrence even though many habitat characteristics are known to influence occurrence of crested newt populations (e.g. [26-28]). Since a species may be found in low quality habitats within a metapopulation (i.e. sinks [7]), we further tested the predictive value of the HSI at a mechanistic level by assessing the relationship between HSI and occurrence of reproduction as well as between HSI and apparent survival.

We selected a HSI for an amphibian species because amphibians are the most endangered vertebrates [29] requiring both terrestrial and aquatic habitats during their life cycles, thus making them a particularly well suited indicator group for habitat quality [30]. Great crested newts are protected under the European Habitats Directive and may serve as umbrella species for wetland conservation [28]. If the HSI can identify habitats where demographic performance is good, it could be used to select habitats harbouring healthy populations (e.g. so called source populations [7]) for conservation purposes. However, if the HSI and demography are unrelated, then this would call for refined habitat suitability models.

Results

We recorded capture histories of 1838 individuals from 2009 to 2011 in our study area, of which 124 individuals were recaptured at least once. Adult newts were captured at 18 sites, ranging from one to 507 individuals per pond. Larvae were found at 13 sites, ranging from one to 105 individuals caught on a single capture event. At six sites we found merely adult newts without larvae whereas only larvae were detected at one pond. At three sites we detected neither adults nor larvae. HSI values ranged from 0.43 to 0.93 in 2009, from 0.41 to 0.93 in 2010 and from 0.44 to 0.94 in 2011 for surveyed sites (Table 1).

Modelling occupancy and reproduction probabilities

We first selected a model that best explained detection probability, while keeping occupancy and reproduction probabilities constant. Akaike model weights (w) suggested that model {ψ (.), R (.), δ_s, $p^{[1]}$ (CE), $p^{[2]}$ (CE)} was best supported by the data ($w = 0.93$; see Additional file 1), whereas remaining models received little support ($w \leq 0.04$). The number of capture events (CE) was included in the top ranking model, indicating that sampling effort positively influences the probability to detect newts in waters occupied without reproduction (logit ($p^{[1]}$) = -1.59 (SE = 1.06) + 0.40 (SE = 0.19) x CE) as well as in waters with successful reproduction (logit ($p^{[2]}$) = 0.72 (SE = 0.63) + 0.38 (SE = 0.20) x CE). The probability of detecting newts was generally higher for a site with reproduction (0.75 - 0.98 for CE = 1–8) than without reproduction (0.23 - 0.83 for CE = 1–8). The probability of correctly identifying sites as breeding sites increased gradually from the start to the end of breeding seasons ($\delta = 0.10$ (SE = 0.07), $\delta = 0.56$ (SE = 0.14), $\delta = 0.80$ (SE = 0.13) and $\delta = 0.89$ (SE = 0.07) for early May, late May, early June and late June, respectively).

In the second step of the analysis, we used the structure of the top-ranking model for detection probabilities and determined the effect of the HSI on ψ and R. Model {ψ (HSI), R (HSI), δ_s, $p^{[1]}$ (CE), $p^{[2]}$ (CE)} best explained the data ($w = 0.77$; Table 2). However, while the effect of the HSI on reproduction probability was well supported by the data, the confidence interval of the estimate of the positive effect of the HSI on occupancy probability included zero (Table 3). The probability of reproduction was higher in ponds with higher HSI values (Figure 1).

Table 1 Number of captured newts (*Triturus cristatus*) and HSI values for 22 sampling sites surveyed between 2009 and 2011

Sampling site	No. of adult newts	Max no. of larvae	HSI 2009	HSI 2010	HSI 2011
1	118	0	0.46	0.46	0.46
2	7	0	0.45	0.41	0.46
4	1	0	0.61	0.61	0.61
8	1	0	0.61	0.61	0.61
9	45	1	0.83	0.82	0.83
10	145	4	0.93	0.93	0.93
11	325	5	0.91	0.93	0.94
12	19	0	0.56	0.56	0.56
13	0	13	0.75	0.76	0.68
13b	104	105	0.93	0.84	0.84
14	191	49	0.79	0.80	0.80
15	27	3	0.83	0.83	0.80
16	0	0	0.47	0.48	0.48
17	52	3	0.78	0.80	0.79
18	122	3	0.76	0.78	0.78
19	0	0	0.43	0.43	0.44
20	79	6	0.82	0.82	0.79
21	57	1	0.66	0.74	0.76
A	8	2	0.50	0.52	0.51
B	32	0	0.53	0.53	0.54
C	507	18	0.55	0.54	0.54
D	0	0	0.48	0.48	0.48

Sampling sites, number of captured adult newts, maximum number of larvae caught on a single capture event and HSI values for 3 years of CMR study (2009–2011).

Table 2 Selection of multiseason-multistate models for estimating occupancy and reproduction probabilities of great crested newts

Model	AIC	ΔAIC	*w*	*K*
ψ (HSI), R (HSI), δ_s, p [1] (CE), p [2] (CE)	261.34	0.00	0.77	12
ψ (.), R (HSI), δ_s, p [1] (CE), p [2] (CE)	263.89	2.55	0.22	11
ψ (HSI), R (.), δ_s, p [1] (CE), p [2] (CE)	269.31	7.97	0.02	11
ψ (.), R (.), δ_s, p [1] (CE), p [2] (CE)	278.04	16.70	0.00	10

Probability of pond occupancy (*ψ*) and probability of reproduction, given presence (*R*) were held constant (.) or modelled as functions of habitat suitability index (HSI). The structure of the top-tanking model for detection probabilities {ψ (.), R (.), δ_s, p [1] (CE), p [2] (CE)} was used to evaluate the effect of HSI on *ψ* and *R*. Probability of correctly identifying a site as breeding site, given successful reproduction (*δ*) was modelled different in each capture period and probabilities of detecting occupancy, given occupancy without reproduction (*p* [1]) and with successful reproduction (*p* [2]) were modelled as functions of the number of capture events per capture period (CE). AIC: Akaike's information criterion; ΔAIC: difference of the AIC value of the current and the best model; *w*: AIC weight; *K*: number of parameters.

Table 3 Parameter estimates (on the logit scale) of the top ranking multiseason-multistate model for estimating occupancy and reproduction of great crested newts

Logit link function	Beta	Estimate	95% CI
logit (ψ_i) = $\beta_{INT} + \beta_{HSI}$ x HSI	β_{INT}	-4.04	-9.27 – 1.20
	β_{HSI}	9.38	-0.36 – 19.12
logit (R_i) = $\beta_{INT} + \beta_{HSI}$ x HSI	β_{INT}	-5.50	-9.70 – 1.29
	β_{HSI}	8.44	2.24 – 14.65

ψ: probability of pond occupancy; *R*: probability of reproduction, given presence. INT: Intercept; HSI: Habitat Suitability Index. CI: confidence interval.

Modelling survival probabilities

The general model with time-dependent apparent survival and recapture probabilities (Φ_t, p_t) fitted the data well (goodness-of-fit test results: $\chi^2 = 7.74$, $DF = 44$, $P = 1$). There was neither evidence for transients (GOF test: $z = 0.36$, $P = 0.72$) nor an effect of capture at a previous occasion (GOF test: $z = -0.48$, $P = 0.63$).

Akaike model weights (w) suggested that the model assuming a seasonal effect on apparent survival {Φ_s, p (.)} was best supported by the data ($w = 0.987$; Table 4). Monthly survival probabilities were lower during the months that newts spend in the pond (aquatic phase; March – June: $\Phi_{aqu} = 0.54$; 95% CI = 0.44 – 0.63) than the months that adults spend in their terrestrial habitat (terrestrial phase; July – February: $\Phi_{terr} = 0.99$; 95% CI = 0.42 – 1.00; Table 5). A model with an effect of HSI on survival probabilities was not well supported by the data (ΔAICc ≥ 8.79). Annual apparent survival was calculated using the formula: $\Phi^4_{aqu} * \Phi^8_{terr}$ [31]. The corresponding standard error was calculated by applying the delta method [32]. Annual survival probability was 0.08 ± 0.0006.

Our estimates of apparent survival were probably distorted by emigration. Apparent survival is the product of true survival and (1 – probability of emigration) [33]. Thus, the annual probability of emigration can be calculated as 1 – (apparent survival / true survival). Based on the annual survival estimate for a metapopulation of crested newts in a similar capture-mark-recapture study [34], we assumed that true survival would be around 0.55. The annual probability of emigration would then be 0.85. If we use annual survival rates 10% lower (0.45) or higher (0.65) than the published estimate [34], then the estimates of the probability of emigration would be 0.82 and 0.87, respectively.

Discussion

HSI and population parameters in great crested newts (*Triturus cristatus*)

Our results suggest that the HSI for great crested newts is not related to survival or pond occupancy

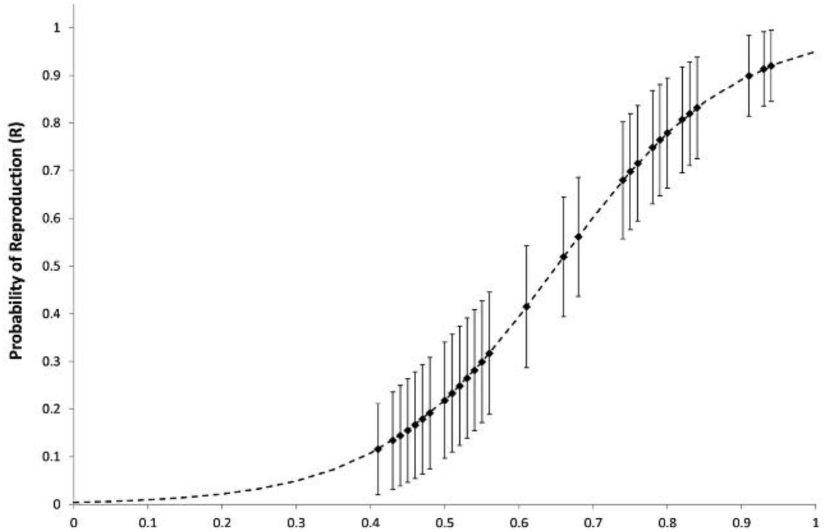

Figure 1 Relationship between HSI and reproduction probability of great crested newts. Symbols represent estimates and SE. Reproduction probabilities were estimated for HSI values observed at 22 ponds over 3 years.

probabilities, but that newt populations are more likely to breed in ponds with higher HSI values. In contrast, [23] showed that there is a positive relationship between the HSI and an index of newt abundance. These results could be misleading, however, for two reasons. First, abundance can be a misleading indicator for habitat quality [6]. Second, imperfect detection was not taken into account [24]. For example, [23] acknowledged that macrophyte cover in ponds may have biased their results. The positive relationship between HSI and abundance reported in [23] could not be confirmed by [25]. In our study, we therefore selected different variables to describe the state of newt populations and we accounted for imperfect detection.

We found that the best multiseason-multistate occupancy model included HSI as covariate for both the probabilities of occupancy (ψ) and of reproduction (R). A previous study which did not differentiate between the presence/absence of adults and larvae [12] found that HSI predicted pond occupancy. In our study, the top-ranking model also included a positive effect of HSI on pond occupancy but the confidence interval of this estimate included zero (Table 3). The comparison of our results with those of [12] shows that differentiating between presence/absence of adults and presence/absence of larvae can give additional insights into habitat suitability. Our results suggest that the HSI is a good predictor for reproduction but not for pond occupancy.

Table 4 Selection of Cormack-Jolly-Seber models for estimating apparent monthly survival of great crested newts

Model	AICc	ΔAICc	*w*	*K*
Φ_s, p (.)	1316.17	0.00	0.987	3
Φ_s (HSI), p (.)	1324.95	8.79	0.012	3
Φ_y, p (.)	1331.27	15.11	0.001	4
Φ_y (HSI), p (.)	1335.81	19.65	0.000	5
Φ (HSI), p (.)	1344.33	28.16	0.000	3
Φ (.), p (.)	1345.94	29.77	0.000	2

Survival probability (*Φ*) was modelled as constant (.), as varying between years (y) or between seasons (s), i.e. during months of terrestrial and aquatic phases of adult newts. In each of this scenarios *Φ* was also modelled as function of habitat suitability index (HSI). Capture probability (*p*) was modelled as constant (.). AICc: corrected Akaike's information criterion; ΔAICc: difference of the AICc value of the current and the best model; *w*: AICc weight; *K*: number of parameters.

Table 5 Parameter estimates of the top-ranking Cormack-Jolly-Seber model for estimating survival probabilities of great crested newts

Model parameter	Estimate	95% CI
Φ_{aqu}	0.54	0.44 – 0.63
Φ_{terr}	0.99	0.42 – 1.00
p (.)	0.07	0.05 – 0.10

Φ_{aqu}: monthly survival probability during aquatic phases of adult newts (March – June); Φ_{terr}: monthly survival probability during terrestrial phases of adult newts (July – February); *p*: capture probability. HSI: Habitat Suitability Index. 95% CI: 95% confidence interval.

We also found newts in ponds with very low HSI values, seemingly not representing suitable habitat (Table 1). Bentonite mats, applied to the soil of one pond in 2001, prevented periodical drying and allowed for the existence of large fish populations. Occasional high water levels led to the colonization of formerly fish-less ponds by native and invasive fish. Fish are well known to negatively affect the distribution and abundance of great crested newts and other amphibians (see reviews in [28] and [35]) which is why the presence of fish leads to lower HSI values for affected ponds (see SI_7). Accordingly, the number of captured newts decreased in those waters over our monitoring period, but still we regularly found some adult newts even in ponds with predatory fish. However, ponds occupied by predatory fish are unlikely to represent suitable habitat for crested newts. Since the goal of HSI models is to predict suitable habitat rather than mere species occurrence, they should not simply indicate whether a pond is occupied or not.

The model developed by [23] emphasizes primarily the aquatic habitat where adult newts congregate for a few months during spring and early summer to reproduce [36]. As would therefore be assumed, our results suggest that the HSI represents a good tool to detect ponds where newts are more likely to reproduce successfully (Figure 1). Hence, it is probable that newts occurring in ponds with lower HSI values do not breed, or that larvae do not survive in these waters until metamorphosis. As spatial variation in newt reproductive success may be common [37], the HSI could allow conservation managers to identify breeding populations or, conversely, populations constituting sinks because of a lack of reproduction [7]. This kind of information is certainly valuable for the effective conservation and recovery of threatened species. Taken together, our results for occupancy and reproduction probabilities suggest that the HSI does a good job because it appears to differentiate between populations with high and low probabilities of reproduction.

If the HSI indicates suitable habitat, then one may expect a positive relationship between HSI and survival. However, we did not find such a relationship (Table 4). Ponds with higher HSI values appear to hold larger populations [23] and survival might be negatively affected by density dependence. Other environmental factors, such as climate may have a stronger effect on survival than habitat quality [34]. To date, there is no data that would allow to test this, or any other hypothesis, for the absence of an effect of the HSI on survival. Remarkably, annual apparent survival was low in our study, suggesting that about 85% of great crested newts may have emigrated. This is an extraordinarily large proportion. However, emigration in the context of our study refers to the place where the newts were captured (i.e. the ponds) and is therefore emigration from the breeding population rather than emigration from the study area. In other words, if a newt did not enter the pond anymore during the three years of our study, it was considered an emigrant. In a short-term study such as ours, it is not possible to distinguish between temporary and permanent emigration [38,39]. Newts may have avoided the ponds and skipped reproduction in the later years of our study in response to the invasion and increase of fish populations. This interpretation of the emigration rate as skipping reproduction in some years is supported by the fact that we observed very few cases of among-pond movement (i.e. 11 individuals). Skipping reproduction might be a strategy to deal with predatory fish because survival on land was high and ponds were temporary, and therefore fish-free, in the past. To test this hypothesis, it would be necessary to extend the mark-recapture study to the terrestrial habitat. To our knowledge, the present study is the first to directly compare survival probabilities during aquatic and terrestrial phases of pond-breeding amphibians. Our study shows that survival probabilities were lower during aquatic than during terrestrial phases of adult great crested newts (monthly survival 54% and 99%, respectively). Monthly survival of 99% (or 92% across the eight months of the terrestrial phase) is unexpectedly high but [40] reported an estimate of annual survival of 99.6% in a cohort of *Ambystoma maculatum* salamanders. While our results suggest that mortality occurs primarily in the water during the breeding season, [36] found that annual survival in a metapopulation of crested newts in the UK was determined by winter weather, i.e. environmental conditions during the terrestrial phase of adults. Hence, factors determining survival may vary spatially [41]. If spatial variation in survival is common, then conservation management should take population-specific differences into account [42].

HSI as a general conservation tool

Habitat suitability models are increasingly applied to wildlife management and conservation planning [3,8]. Guisan et al. [3] outlined the steps that are necessary to increase the use of such models to guide conservation decisions. They noted that modelled occurrence probabilities do not always correlate with demographic processes determining population viability [21,43], a finding we regard to be of particular importance for the use of HSI models in conservation practice. We suggest that a focus on the occurrence of a species may not always provide the best models for conservation applications. First, a species may occur in sink habitats [7] and second, a species may not occur in suitable patches as a consequence of extinction and colonization dynamics in metapopulations [18] or due to interspecific competition [19]. Consequently, it is not surprising that many studies did not find the expected correlation between modelled habitat suitability and individual performance, demography or population viability ([9, 11, 17 and references in [3]). Establishing a link between reproduction and habitat suitability seems to be an important step forward [14]. We suggest that modelling the probability of reproduction rather than the probability of occurrence in habitat suitability models using techniques that estimate a true probability rather than a relative suitability score might give valuable additional insights [44-47]. This might be a better way to identify suitable habitat and to increase the utility of these models for conservation.

Conclusions

HSI models are increasingly applied as predictive tools for management purposes, assuming that habitat suitability predicts species performance and demography. However, the validity of this assumption has rarely been evaluated. We studied the relationship between a commonly used HSI [23] and occurrence/demographic parameters in a pond-breeding amphibian protected under the European Habitats Directive, the great crested newt (*Triturus cristatus*). Our results show a positive relationship between the HSI and reproduction probability (i.e. the occurrence of larvae), whereas pond occupancy and survival probabilities were not related to HSI. This is both good and bad news for conservation managers. The good news is that HSI models may indicate breeding populations rather than mere species occurrences, thus identifying habitats of higher priority for conservation purposes. Modelling breeding populations vs. non-breeding populations rather than presence/absence data might help to identify habitats harbouring healthy populations and to improve the utility of HSI models for the conservation of threatened species (for similar conclusions, see [48,49]). The bad news is that the most suitable habitat is not necessarily the habitat where demographic performance is best. Since there may be no direct link between habitat suitability and demographic processes determining population viability, we recommend that conservation practitioners should use HSI models cautiously.

Methods

Study species and determination of HSI

The great crested newt (*Triturus cristatus*) is a pond-breeding amphibian species, listed in Annexes II and IV of the European Habitats Directive (92/43/EEC). EU member states are therefore required to monitor the conservation status of this species. Accordingly, monitoring and management of great crested newt populations would benefit from informative and easily applicable tools and consequently, from a validated HSI. The HSI for the great crested newt incorporates ten habitat features (see Additional file 2; [23]), which are assessed for a pond and converted to suitability index (SI) scores on a scale from 0.01 to 1.0. SIs are site location relative to species distribution (i.e. whether a population occurs at the edge or in the centre compared to the distributional range; SI_1), pond area (SI_2), pond permanence (SI_3), water quality (SI_4), shading of pond perimeter (SI_5), number of water fowl per 1000 m^2 (SI_6), impact of fish (SI_7), pond density within a radius of 1 km (SI_8), proportion of suitable terrestrial habitat within surrounding 500 m (SI_9) and macrophyte cover (SI_{10}). The HSI for great crested newts is calculated as geometric mean of these ten suitability indices:

$$HSI = (SI_1 * SI_2 * SI_3 * SI_4 * SI_5 * SI_6 * SI_7 * SI_8 * SI_9 * SI_{10})^{1/10}$$

We calculated the HSI for each pond in each year of the study. Since this index was originally developed for the UK, we had to transfer the statements regarding the location relative to species distribution (SI_1) to Germany. According to [23], study sites with a high probability of great crested newt occurrence within each 10 km square are scored with 1.0 for SI_1 and sites with a low probability of newt occurrence are scored with 0.5. Within Germany, our study sites are located in an area of an intermediate probability of newt occurrence. Therefore, we fixed SI_1 to 0.75 for all ponds. Since the original HSI [23] only provides values for ponds of an area of up to 2000 m^2, we had to omit SI_2 for eight ponds of greater size and calculated the ninth rather than the tenth root of the product instead.

Study area and sampling procedure

We conducted a capture-mark-recapture (CMR) study and surveyed 22 lentic water bodies in a former flooding area of the Rhine river near Krefeld, Germany (coordinates: 51°19'5" N, 6°39'17" E; Figure 2; Additional file 3), for the presence of great crested newts. The study area is primarily dominated by grasslands, woodlands and wetlands. The northern part, however, is also influenced by adjacent residential areas and agriculture. Adult and larval crested newts can easily be captured with traps in ponds during the breeding season from March to July [50]. Detection or non-detection of adults and larvae was recorded during multiple capture events from March to June in 2009 and 2010 as well as from April to June in 2011. Several visits to each water body were essential to distinguish between sites where great crested newts did not occur and sites where this species has been overlooked [51]. Therefore, every site was visited between 12 and 66 times during the 3 years of monitoring. Newts were

Figure 2 Overview of the study area near Krefeld (Germany). Illustrated are all 22 surveyed ponds which are mainly located within the FFH-area of the "Latumer Bruch" (DE-4605-301; coordinates: 51°19′5″ N, 6°39′17″ E).

captured using Ortmann's funnel traps [52], which were constructed of empty 10 liter paint buckets with four distinct openings in which half-cut inverted 1.5 liter plastic bottles were inserted functioning as funnels. These traps were evenly distributed along the shoreline and remained in the water for 48 hours. The number of traps deployed per capture event varied according to pond area, ranging from one to 36 traps. After data collection, all individuals were released immediately.

To allow individual recognition during the CMR study, we used photographs of the ventral side of newts, which provides a highly variable but individually unique and lifelong permanent colour pattern [53]. Recaptured individuals were identified automatically by the program AMPHIDENT [54]. AMPHIDENT can reliably detect recaptures even in large datasets based on a cross-correlation comparison algorithm (>1500 individuals; [55]).

Modelling occupancy and reproduction probabilities

We used multiseason-multistate occupancy models [43,44] to estimate the probability that great crested newts occur in a water body (ψ) and the probability that newts reproduced successfully (R). The model assumes that sites fall into one of three categories: absence of the species, presence without production of offspring, and presence with production of offspring. With this model, we can model both the presence/absence of newts and the presence/absence of reproduction (given occurrence). We used the presence/absence of larvae as a proxy for production of offspring (i.e. the probability that newts reproduced successfully; larvae are more likely to indicate successful recruitment than the presence of eggs). Unlike models based on presence-only data, which estimate a habitat suitability score, these models estimate true probabilities [46]. Sampling effort varied between sites, ranging from three to 45 capture events during the entire breeding seasons. Therefore, repeated detection/non-detection data were simplified for analysis as follows. For each breeding season per year (i.e. primary period) we defined four capture periods (two-week periods: 1–15 May, 16–31 May, 1–15 June and 16–30 June). If a site was not visited during a capture period, this was treated as a missing observation. If multiple capture events were conducted within a capture period, a site was classified as state $m = 0$ if no newts were detected, as state $m = 1$ if at least one adult was found and as state $m = 2$ if at least one larva was detected. Accordingly, every site received a specific detection history like 1022 0112 0122, where 1 indicates that adults were detected, 0 indicates that neither adults nor larvae were found and 2 indicates that larvae were detected. In this way, we retained as much data as possible without having too many missing observations within a given sampling season [56]. Because of this simplification, we used capture effort (CE = number of capture events per capture period) as explanatory variable for detection probability.

We used a two-step approach to model selection. We first modelled the detection process and then the probabilities of site occupancy and reproduction. We developed an *a priori* candidate model set (see Additional file 1) to select a best model for the probability of detecting occupancy given that a site was occupied without reproduction ($p^{[1]}$), the probability of detecting occupancy given that a site was occupied with successful reproduction ($p^{[2]}$) and the probability of correctly identifying a site as breeding site given that successful reproduction did occur (δ). To identify the best detection model we held occupancy parameters (ψ and R) constant and evaluated the effect of capture effort on $p^{[1]}$ and $p^{[2]}$, allowing δ to vary in time. We hypothesized that $p^{[1]}$ and $p^{[2]}$ are influenced by capture effort (CE), because a higher sampling effort should result in a higher probability of detecting species occurrence. This variable accounts for the fact that the number of capture events varied both within and between ponds. Moreover, we allowed δ to vary between May and June (δ_m) as well as between capture periods (δ_s), since larvae should be more abundant and bigger later in the season and are therefore easier to detect.

In the second step, we determined the effect of the HSI on occupancy probability (ψ) and reproduction probability (R), while using the best model for the detection parameters as determined in the first step. Since we were mainly interested in the influence of the HSI on occupancy and reproduction probabilities rather than in state transitions between years, we modelled variables describing changes over time (parameters ψ^{m}_{t+1} and R^{m}_{t+1} in the transition probability matrices [45], with m = state) in the same way as the initial variables ($\psi_{t=1}$ and $R_{t=1}$). Overall, four different models were considered: a) both ψ and R were modelled as constant; b) both ψ and R were modelled as functions of the HSI; c) ψ was modelled as constant and R was modelled as a function of the HSI; d) ψ was modelled as a function of the HSI and R was modelled as constant. We hypothesized that sites with a higher HSI value should have higher probabilities of occupancy and reproduction. Statistical models were implemented in program Presence 6.2 [57].

Modelling survival probabilities

We used Cormack-Jolly-Seber models [58] to estimate monthly survival and detection probabilities (Φ and p). Capture data were pooled for the months March, April, May and June. If a water body was not visited during a month, detection probability p was set to 0 for this site and period. If multiple capture events were conducted within a month, only the first capture of individuals was counted. Pooling data from several consecutive capture occasions within a month generally increases precision but may induce some bias in survival estimates [59-61]. Overall, adults were captured in 18 out of 22 water bodies (Table 1). However, at two of these 18 sites only one adult was detected, both only once in April 2010. Neither individual was ever recaptured again during the entire sampling period. Therefore, we excluded these two ponds from the mark-recapture analysis and estimated survival probabilities at 16 different sites. Data were too sparse to include covariates for detection probability. Therefore, detection probability (p) was always held constant even though this model may not be the best description of the observation process. Survival probabilities (Φ) were modelled either as constant, as varying between years, or as varying between aquatic (March - June) and terrestrial (July - February) phases of adult newts (survival was assumed to be constant within both the aquatic and the terrestrial phase). In the latter case, the specification of the unequal time intervals between capture occasions allowed for the calculation of monthly survival estimates.

For each of these scenarios, we also allowed Φ to be a function of the covariate HSI. We hypothesized that there is a positive correlation between the HSI and survival probabilities. Models were implemented in program MARK 6.2 [62].

Since only 11 individuals were recaptured at different sites and therefore moved from one site to another, we did not attempt to estimate dispersal probability. If an individual was detected at a new site, then it was scored as having died at the first site (by assigning "-1" to the capture history) and entered as a new individual at the new site.

Model selection and model notation

Model selection was based on Akaike's information criterion (AIC [63]). The model with the lowest AIC (or AICc) was considered the most parsimonious model given the data. We also used Akaike weight (w) as a measure of relative support for each model.

Our model notation system follows the standard notation of [58] and [64] providing information about the sources of variation used to model each parameter. The term (.) indicates that a parameter was held constant (i.e. no covariates).

Additional files

Additional file 1: Model selection of multiseason-multistate models for estimating detection parameters of great crested newts.

Additional file 2: Ten Suitability Indices (SI) for the calculation of the HSI for great crested newts according to Oldham et al. (2000).

Additional file 3: Distance matrix [km] of surveyed ponds.

Competing interests
The authors declare that they have no competing interests.

Authors' contributions
BU performed the statistical analysis and drafted the manuscript. BRS and SS conceived and designed the study and helped to draft the manuscript. AD conducted the field work. All authors read and approved the final manuscript.

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Additional file 1: Model selection of multiseason multistate models for estimating detection parameters of great crested newts.

Model	AIC	ΔAIC	*w*	*K*
ψ (.), R (.), δ_s, $p^{[1]}$ (CE), $p^{[2]}$ (CE)	278.04	0.00	0.93	10
ψ (.), R (.), δ_m, $p^{[1]}$ (CE), $p^{[2]}$ (CE)	284.13	6.09	0.04	8
ψ (.), R (.), δ_s, $p^{[1]}$ (.), $p^{[2]}$ (.)	285.46	7.42	0.02	8
ψ (.), R (.), δ_m, $p^{[1]}$ (.), $p^{[2]}$ (.)	291.53	13.49	0.00	6
ψ (.), R (.), δ (.), $p^{[1]}$ (CE), $p^{[2]}$ (CE)	303.64	25.60	0.00	7
ψ (.), R (.), δ (.), $p^{[1]}$ (.), $p^{[2]}$ (.)	311.31	33.27	0.00	5

Probability of pond occupancy (ψ) and probability of reproduction, given presence (R) were held constant (.) to evaluate the effects of sampling effort and sampling time on detection parameters. Probability of correctly identifying a site as breeding site, given successful reproduction (δ) was modelled as constant (.) or was allowed to vary between capture periods (s) or between months (m). Probabilities of detecting occupancy, given occupancy without reproduction ($p^{[1]}$) and with successful reproduction ($p^{[2]}$) were modelled as constant (.) or as functions of the number of capture events per capture period (CE). AIC: Akaike's information criterion; ΔAIC: difference of the AIC value of the current model and of the best model; *w*: AIC weight; K: number of parameters.

Additional file 2: Ten Suitability Indices (SI) for the calculation of the HSI for great crested newts according to Oldham *et al.* (2000).

SI	Factor	Explanation
SI_1	Geographic location	Location of the population relative to species national distribution
SI_2	Pond area	Pond surface area (m^2)
SI_3	Pond permanence	Frequency of pond drying per decade
SI_4	Water quality	Water quality determined by using invertebrate diversity
SI_5	Pond Shading	Percentage of perimeter shaded to at least 1m from shore
SI_6	Water fowl	Number of water fowl seen per $1000m^2$
SI_7	Fish	Occurrence and species composition of fish populations
SI_8	Pond density	Number of ponds occurring within $1km^2$ of survey pond
SI_9	Proportion of "newt friendly" habitat	Amount of shelter and foraging opportunities offered by the terrestrial habitat within 500m surrounding the pond
SI_{10}	Macrophyte content	Percentage of pond surface area occupied by macrophyte cover

SI: Suitability Index.

Additional file 3: Distance matrix [km] of surveyed ponds.

	1	2	4	8	9	10	11	12	13	13b	14	15	16	17	18	19	20	21	A	B	C	D
1	0.00																					
2	0.33	0.00																				
4	0.70	0.37	0.00																			
8	1.20	0.93	0.66	0.00																		
9	1.60	1.34	1.07	0.42	0.00																	
10	1.64	1.40	1.14	0.48	0.13	0.00																
11	2.25	2.01	1.76	1.10	0.70	0.62	0.00															
12	2.29	2.03	1.73	1.10	0.68	0.65	0.28	0.00														
13	1.84	1.72	1.62	1.07	0.92	0.79	0.86	1.11	0.00													
13b	2.05	1.95	1.87	1.32	1.15	1.03	0.98	1.25	0.25	0.00												
14	2.32	2.23	2.16	1.62	1.43	1.31	1.17	1.45	0.55	0.30	0.00											
15	2.39	2.31	2.24	1.70	1.51	1.39	1.23	1.51	0.63	0.38	0.08	0.00										
16	2.21	2.33	2.49	2.29	2.36	2.27	2.45	2.70	1.59	1.49	1.44	1.43	0.00									
17	2.04	2.12	2.24	1.99	2.04	1.94	2.10	2.35	1.24	1.15	1.12	1.12	0.34	0.00								
18	2.13	2.22	2.35	2.12	2.17	2.07	2.23	2.48	1.38	1.27	1.23	1.23	0.22	0.13	0.00							
19	1.26	1.19	1.19	0.86	0.97	0.90	1.30	1.47	0.62	0.80	1.06	1.13	1.43	1.13	1.26	0.00						
20	1.19	1.13	1.15	0.87	1.02	0.95	1.37	1.54	0.70	0.88	1.13	1.20	1.42	1.13	1.25	0.08	0.00					
21	2.97	2.90	2.83	2.27	2.04	1.92	1.61	1.89	1.21	0.96	0.67	0.59	1.69	1.45	1.51	1.72	1.78	0.00				
A	1.21	1.42	1.69	1.78	2.04	1.99	2.43	2.60	1.66	1.74	1.88	1.92	1.11	1.08	1.11	1.13	1.06	2.41	0.00			
B	1.84	2.00	2.21	2.11	2.27	2.19	2.47	2.70	1.62	1.59	1.62	1.64	0.45	0.55	0.52	1.29	1.26	2.00	0.68	0.00		
C	0.64	0.86	1.15	1.37	1.71	1.69	2.23	2.34	1.60	1.75	1.97	2.03	1.59	1.46	1.53	0.99	0.90	2.58	0.57	1.20	0.00	
D	0.33	0.66	1.03	1.48	1.87	1.89	2.48	2.55	1.98	2.17	2.41	2.48	2.09	1.97	2.04	1.37	1.29	3.04	1.02	1.69	0.51	0.00

Pairwise distance between centers of ponds in kilometres. Darker shadings indicate greater distance.

Chapter II

The relationship between habitat suitability, population size and body condition in a pond-breeding amphibian

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The relationships between habitat suitability, population size and body condition in a pond-breeding amphibian

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Abstract

The ecological niche of a species determines whether a species can persist and reproduce in a patch or not. The niche of a species is often described using habitat suitability models and indices. Accordingly, one may expect tight links between demography, phenotypes of individuals, population size, and habitat suitability. However, such links are not always found. Here, we study the relationship between a habitat suitability index that is commonly used for conservation assessments and metrics describing the performance at the level of populations and individuals. Using data from a metapopulation of a pond-breeding amphibian, the Great Crested Newt (*Triturus cristatus*), we show that habitat suitability predicts population size but not body condition. Ponds with higher suitability had a higher population size of newts, whereas population size correlated negatively with body condition of individuals. Our results are in line with previous studies showing no straightforward relationship between habitat suitability and body condition (a measure of individual performance) and the performance of populations. We suggest that a population size-dependent reduction of body condition may be a regulatory mechanism in newt populations.

Keywords: *Triturus cristatus*; Phenotypic trait; Ecological niche; Demography

Introduction

The Hutchinsonian population-persistence niche determines whether or not a species can occur and persist in a habitat patch because its population growth rate is either positive or negative (Chase 2011; Hooper et al. 2008; Schoener 2009). The ecological niche of a species is often described

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using statistical models linking data on species presence or abundance to environmental data (known as habitat suitability models, species distribution models or ecological niche models; Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Guillera-Arroita et al. 2015). The output of these models is a habitat suitability score. A natural assumption is that individuals and populations fare better where the habitat is more suitable for the species. This can be seen in Van Horne's (1983) definition of habitat suitability which is "the product of density, mean individual survival probability and mean expectation of future offspring". The relationship between habitat suitability and abundance and demography matters, for example, when estimates of habitat suitability are used to inform conservation decisions (Guisan et al. 2013). As Guisan et al. (2013) note, habitat suitability based on the modelled relationship between occurrence records and the environment may not always correlate with population state variables (e.g. population size, demography and phenotypes) necessary for population persistence. This might result from the fact that species can be found in unsuitable habitat patches (e.g., population sinks; Pulliam 2000) or species may be absent from suitable patches in metapopulations (Hanski 1998). Unsurprisingly, some previous studies found a correlation between habitat suitability and population state variables whereas others did not (Bean et al., 2014; Boiffin, Badeau, & Bréda 2017; Diez, Giladi, Warren, & Pulliam 2014; Thuiller, Albert, Dubuis, Randin, & Guisan 2010; Unglaub, Drechsler, Steinfartz, & Schmidt 2015; Whitman & Ackerman 2015; Wright, Davies, Lau, McCall, & McKay 2006). We believe that it is of fundamental importance for basic and applied ecology to understand the relationships between niche, habitat suitability and population and individual state variables (Matthiopoulos et al. 2015; Schurr et al. 2012; Thuiller et al. 2010; Thuiller et al. 2014).

Using a pond-breeding amphibian as a model, Unglaub et al. (2015) showed that a commonly used habitat suitability index predicted neither pond occupancy nor individual survival. Instead, habitat suitability could be used to predict the ponds where reproduction occurred. Here, we study the relationship between habitat suitability, population size and body condition (i.e., a measure of individual performance) in a metapopulation of the Great Crested Newt (*Triturus cristatus*), a threatened pond-breeding amphibian. We argue that it is important to use both individual-level and population-level metrics to assess and understand habitat suitability because effects on individuals will not necessarily have an effect at the population level (McPeek & Peckarsky 1998; Vonesh & De la Cruz 2002). Moreover, habitat suitability may affect abundance and phenotypic traits differently (Ousterhout et al. 2015), and phenotypic traits of individuals can affect population dynamics and vice versa (Ozgul et al. 2010). Linking abundance rather than occurrence to habitat suitability may be of greater interest to ecologists and conservation biologists because spatial variation in abundance contains more information than occurrence data (Royle, Nichols, & Kéry 2005). However, population size should not be used as the sole metric to describe habitat suitability (Van Horne 1983). We decided to use body condition as an individual-level metric to assess habitat suitability (Bean et al. 2014; Johnson 2007) because a negative relationship between abundance and body size has been reported in previous studies (Green & Middleton 2013; Ousterhout, Anderson, Drake, Peterman, & Semlitsch 2015; White, Ernest, Kerkhoff, & Enquist 2007). In amphibians in general and in newts in particular, body condition is an important phenotypic trait that is related to environmental variation, habitat quality, individual survival, and sexual selection (Green 1991; Janin, Léna, & Joly 2011; Reading & Clarke 1995; Reading 2007; Scheele et al. 2014).

We tested whether habitat suitability has positive effects on both population size (as originally suggested by Oldham, Keeble, Swan, & Jeffcote 2000) and body condition. Alternatively, there may be a positive effect of habitat suitability on population size only, and a negative effect on body condition because increased population size may lead to lower per-capita resource availability. Testing which pattern holds true appears crucial for our understanding of habitat suitability.

Materials and methods

Study species

Great Crested Newts (*Triturus cristatus*) are among the most prominent pond-breeding amphibian species in Europe. They reach up to 20 cm in total body length, with females being generally larger than males. Males display a high dorsal crest as part of the species' sexual dimorphism during the time of reproduction (Jehle, Thiesmeier, & Foster 2011). Adult, juvenile, and larval Crested Newts can easily be captured with traps in ponds during the breeding season (March to July; Jehle et al. 2011). Great Crested Newts are listed in Annexes II and IV of the European Habitats Directive (92/43/EEC). EU member states are required to monitor the conservation status of this species. Great Crested Newts are on the Red Lists of many European countries (Dufresnes & Perrin 2015).

Study area and sampling procedure

We conducted a capture-mark-recapture study in 41 lentic water bodies within the adjacent nature reserve areas Höltigbaum and Stellmoorer Tunneltal which are located in the north of Hamburg, Germany (53° 37′ 32″ N, 10° 12′ 18″ E; Fig. 1). The study area covers 743 hectares. The main habitat and land use types are pasture, riparian forests, reeds, fallows, dry meadows, broadleaf forests, and a variety of small water bodies.

In 2012, we captured newts during two sessions, one early (April/May) and one late (June/July) in the breeding season. Each capture session consisted of three consecutive days of capturing newts, giving us a total of six capture events for each pond in a "robust design" format (Williams, Nichols, &

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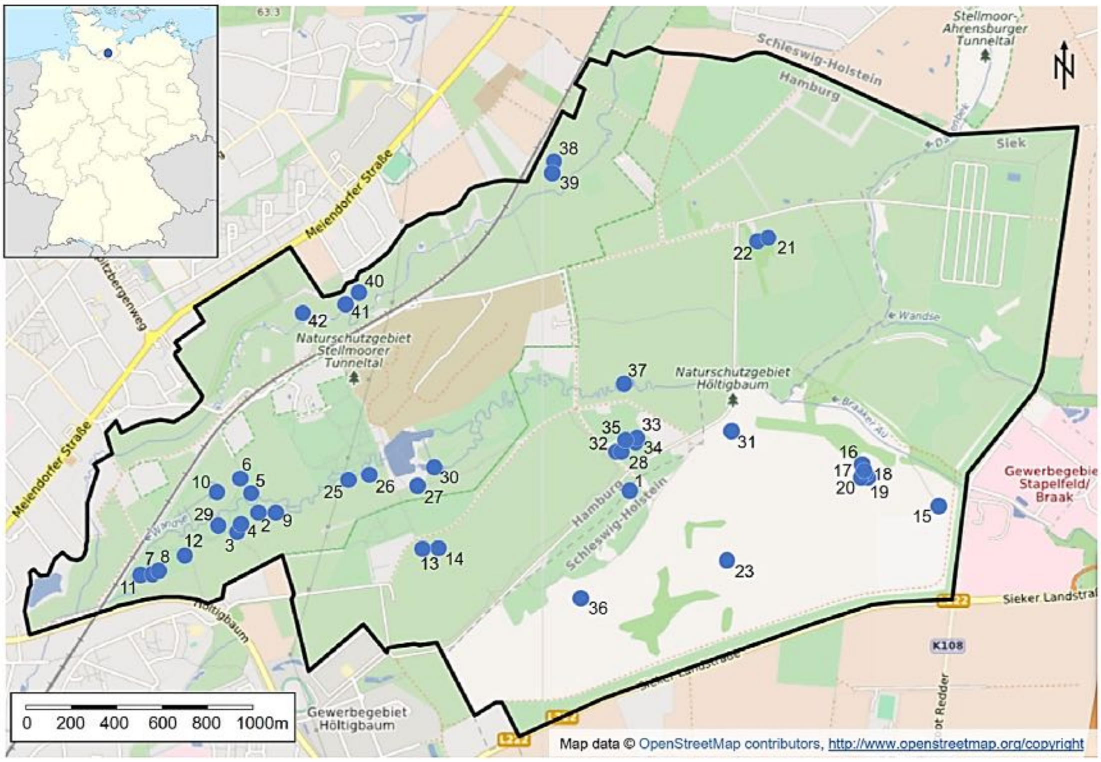

Fig. 1. Map of the study area. Ponds are shown as numbered blue dots. The inset shows the location of the study area in Germany. The map was made with data provided and copyrighted by OpenStreetMap available under the Open Database License (https://www.openstreetmap.org/copyright).

Conroy 2002). We used the mark-recapture data to estimate survival and detection probabilities as well as population size.

Newts were captured using Ortmann's funnel traps (Drechsler, Bock, Ortmann, & Steinfartz 2010). Traps were evenly distributed along the shoreline of ponds and remained in the water for 48 h. The number of traps deployed per capture event varied according to pond surface area, ranging from one to 27 traps. In order to allow for individual recognition, we used digital photographs of the ventral colour pattern of each newt. The ventral colour pattern is highly variable among individuals, but unique and stable for each individual allowing for reliable lifelong identification (Hagström 1973). Captured individuals were identified and recognized automatically from digital images by the program AMPHIDENT (Drechsler, Helling, & Steinfartz 2015).

Body condition

We measured snout-vent length and body mass of 1400 adult and 83 juvenile Great Crested Newts. For the calculation of body condition indices, the body mass (W) of each individual was measured to the nearest 0.1 g with a portable micro scale (Voltcraft, PS-20). Snout-vent length (SVL) was measured with a ruler to the nearest 0.1 cm. We used three different condition indices commonly applied to aquatic and semi-aquatic ectotherms (Bancila, Hartel, Plaiasu, Smets, & Cogalniceanu 2010): Fulton's index (K) was calculated as $K = (W/SVL^3) * 100$. After $\log_{10}$-transformation of the data, body mass was regressed on body size. The relative weight index was calculated as $W_r = (W/W_s) * 100$ where W is the observed weight of an individual and W_s is the predicted weight from the linear regression. The residuals of this regression were used for the body condition index R_i.

Snout-vent lengths of males (mean ± SE = 6.70 ± 0.02 cm; $n = 683$), females (mean ± SE = 7.06 ± 0.02 cm; $n = 716$), and juveniles (mean ± SE = 5.17 ± 0.05 cm; $n = 84$) were significantly different (males vs. females: $U = -11.611$; $p = 2.84 * 10^{-30}$; males vs. juveniles: $U = -14.693$; $p = 7.10 * 10^{-49}$; females vs. juveniles: $U = -14.891$; $p = 3.77 * 10^{-50}$). Also, body mass of males (mean ± SE = 7.72 ± 0.06 g), females (mean ± SE = 8.59 ± 0.07 g), and juveniles (mean ± SE = 3.86 ± 0.12 g) differed significantly (males vs. females: $t = -8.783$; $p = 4.62 * 10^{-18}$; males vs. juveniles: $t = 28.245$; $p = 4.62 * 10^{-18}$; females vs. juveniles: $t = 33.339$; $p = 1.29 * 10^{-72}$). Therefore, we regressed log (W) on log (SVL) and calculated W_r and R_i for each of these groups, separately (see Fig. S1 in Supporting Information).

Estimating detection probabilities and population size

A full mark-recapture analysis of the newt metapopulation will be presented elsewhere (Unglaub et al., unpublished manuscript). Here, we used the mark-recapture data to estimate population size using the estimator of Wood, Nichols, Percival, & Hines (1998). Using the estimated detection probabilities from the mark-recapture survival analysis (Lebreton, Burnham, Clobert, & Anderson 1992), the population size (N_{ij}) of Great Crested Newts in pond i and capture session j (with "early" = April/May and "late" = June/July) was estimated using the equation: $N_{ij} = n_{ij}/p_{ij}$, where n_{ij} is the number of captured adult newts and p_{ij} is the estimated detection probability (Wood et al. 1998; these authors also provide an equation for the standard error). Great Crested Newts were captured in 32 different ponds. Nine ponds were excluded from the mark-recapture analysis because no recaptures were made.

We analyzed the capture-recapture data of 1427 individuals (662 males, 693 females and 72 juveniles) using Cormack–Jolly–Seber models (Lebreton et al. 1992) to estimate apparent survival (Φ), detection probabilities (p) and population size of newts in 23 ponds. We accounted for the unequal time intervals between capture sessions and estimated daily survival probabilities during the breeding season. Since only five individuals were recaptured at different ponds (sites) after having migrated to a different pond, we did not attempt to estimate movement probabilities. If an individual was detected at a new site, then it was scored as having died at the first site (by assigning "−1" to the capture history) and recorded as a new individual at the new site.

We fitted a small number of models to the data such that we could use model-averaged estimates of detection probability for the estimation of population size. Apparent survival (Φ) was modelled as either constant (.) or as a function of one of the three body condition indices K, W_r or R_i. Detection probabilities (p) were modelled as either constant (.), as varying between capture sessions (early vs. late; *seas*), as varying between different ponds (g) or as varying between capture sessions as well as between different ponds (g*seas*). If a pond dried out during the sampling period, p was set to 0 for this pond and capture session.

Models were implemented in MARK 6.2 (White & Burnham 1999). Our model notation system follows the standard notation of Lebreton et al. (1992). Model selection was based on the corrected Akaike's information criterion (AICc; Burnham & Anderson 2002). We also used Akaike weight (w) as a measure of relative support for each model.

Determination of habitat quality

Habitat quality is often evaluated by using habitat suitability indices (HSI). An HSI is a numerical index, ranging from 0 (unsuitable habitat) to 1 (optimal habitat). The HSI for the Great Crested Newt was developed by Oldham et al. (2000) and incorporates ten habitat features which are assessed for a pond and converted to suitability index scores (SI) on a scale from 0.01 to 1.0. Habitat features comprise, (1) site location relative to species distribution (i.e. whether a population occurs at the edge or in the centre compared to the distributional range), (2) pond area, (3) pond permanence, (4) water quality, (5) shading of pond perimeter, (6) number of water fowl per 1000 m^2, (7) impact of fish, (8) pond density within a radius of 1 km, (9) proportion of suitable terrestrial habitat within surrounding 500 m and 10) macrophyte cover. The HSI for the Great Crested Newt is then calculated as geometric mean of these ten suitability indices:

$$HSI = (SI_1 * SI_2 * SI_3 * SI_4 * SI_5 * SI_6 * SI_7 * SI_8 * SI_9 * SI_{10})^{1/10}$$

Since this index was originally developed for Great Crested Newts in the UK and only provides values for ponds of an area of up to 2000 m^2, we had to make some necessary adaptions to fit the situation for studied sites in Germany (see Unglaub et al. 2015). First, we set SI_1 constant to 0.75 for all ponds in our study. Second, we omitted SI_2 for four ponds larger than 2000 m^2 and then calculated the ninth rather than the tenth root of the product instead.

Habitat suitability, population size and body condition

First, we conducted an analysis at the pond level to test whether HSI affected population size. Because we had two population size estimates for some of the ponds (early and late in the season), we used a linear mixed model with pond ID as a random effect. Population size was log-transformed for the analysis to obtain predicted values ≥ 0.

In the second analysis, at the level of individuals, we used linear mixed models to analyze the relationships between HSI, population size and body condition. Where available, we used the two population size estimates per pond and used sex as an individual-level and reproductive status as a population-level explanatory variable. Population size was standardized prior to analysis. Reproductive status of the population was a binary variable indicating whether or not we found larvae in the pond. To account for changes in body condition within the season, we included a factor describing whether the measurements were taken early or late in the season. Pond was included as a random factor to account for non-independence of individuals inhabiting the same pond.

We repeated the analysis for all three body condition indices. Models were fitted to the data in R using the package "lme4" (Bates, Maechler, Bolker, & Walker 2015; R Core Team 2017). We used the sim() function in the package "arm" (Gelman et al. 2015) to predict and plot regression lines and confidence intervals.

Alternatively, one may analyze density (i.e., population size/area) rather than population size, i.e. add pond area to the models. We did not do so because pond area is one of the factors included in the calculation of the HSI (HSI and pond area are correlated: $r = 0.52$; low HSI values are unlikely if the pond area is large). For body condition, results were qualitatively similar when we added pond area to the models. In the population-level analysis, however, the effect of HSI on abundance was not significant, even though the coefficient was still positive (beta = 3.59 (95% CI: −0.77, 7.95).

For a subset of the adult animals ($n = 24$), we tested whether there was a correlation between body condition and age. We used skeletochronology to determine age (Sinsch 2015). Age determination is based on the number of lines of arrested growth (LAG) in the phalanges and is a reliable measure of age in short-lived animals such as Great Crested Newts (Sinsch 2015). For age determination, the fourth toe of the right hind limb of individuals was clipped and stored in 4% formaldehyde. Preserved toes were soaked in distilled water before decalcification with 2% nitric acid. The acid solution was removed in several rinses with distilled water. Samples were then dehydrated in an alcohol series (30%, 50%, 70%, 90%, 96%, 99.8% ethanol, at least 2 h each), followed by an isopropanol step, and subsequently embedded in paraffin. Embedded phalanges were cross-sectioned at mid-diaphyseal level. Sections (thickness: 10 μm) were stained with Ehrlich's haematoxylin. For each bone, several cross sections were examined using a microscope slide scanner (Leica DM6000 B; Leica Microsystems GmbH) and LAGs were counted. Median age was 3 (interquartile range: 2–4). Correlation coefficients were −0.02, 0.20, and 0.35 for the three estimates of body condition. There was also no effect of age on body condition when we accounted for difference in pond of origin (as a random effect), sex and capture session (early or late).

Results

Estimating apparent survival, detection probabilities, and population size

There was strong support that detection probabilities varied between ponds and capture sessions (summed Akaike weights: $w = 1$; Table 1). Models assuming either of these effects without the other or constant detection probabilities received no support given the data ($w = 0$). Among the models considered, the model assuming constant survival and varying detection probabilities for different ponds and capture sessions $\{\Phi\ (.), p\ (g * seas)\}$ was best supported by the data ($w = 0.47$; Table 1). Models that included an effect of body condition on survival were not well supported by the data ($w = 0.19$ for K, $w = 0.17$ for R_i and $w = 0.17$ for W_r, respectively) and the confidence interval of the beta estimates of the three condition indices included zero (see Table S1 in Supporting Information).

Table 1. Selection of Cormack–Jolly–Seber models for estimating apparent daily survival and detection probabilities of Great Crested Newts during breeding season. AICc of the best model was 1988.45. Survival probability (Φ) was modelled as constant (.) or as a function of the covariates K, W_r or R_i. Capture probability (p) was modelled as constant (.), as varying between capture sessions early (April/May) and late (June/July) in the season (*seas*), as varying between different ponds (g) or as varying between different ponds as well as between capture sessions (g*seas*). Only models with $w > 0.01$ are shown. K: Fulton's index. W_r: relative mass condition index. R_i: residual condition index. AICc, corrected Akaike's information criterion; ΔAICc, difference of the AICc value of the model with the lowest AICc score and the given model; w, Akaike weight; np, number of parameters.

Model	ΔAICc	w	np
Φ (.) p (g*seas*)	0.00	0.46590	41
Φ (K) p (g*seas*)	1.84	0.18621	42
Φ (R_i) p (g*seas*)	1.98	0.17390	42
Φ (W_r), p (g*seas*)	1.98	0.17298	42

Table 2. Model averaged detection probabilities (p), number of captured individuals (K) and estimated population size (N) per pond and capture session (SE: standard error). Estimates of population size (and the associated SE) are rounded to the nearest integer. N/A: parameter not estimable.

Pond	April/May			June/July		
	p (SE)	K	N (SE)	p (SE)	K	N (SE)
1	0.09 (0.03)	83	877 (279)	0.03 (0.02)	16	552 (327)
3	0.07 (0.06)	31	469 (455)	0.07 (0.04)	11	157 (93)
4	0.03 (0.03)	45	1629 (1608)	0.08 (0.03)	59	713 (239)
5	N/A	12	N/A	0.06 (0.06)	7	118 (120)
6	0.06 (0.03)	85	1425 (620)	0.06 (0.02)	55	884 (303)
7	0.26 (0.23)	2	8 (7)	N/A	3	N/A
13	0.09 (0.03)	76	888 (322)	0	0	0
14	0.18 (0.06)	30	165 (57)	0.15 (0.07)	8	54 (26)
15	0.11 (0.03)	109	954 (285)	0.02 (0.01)	5	290 (210)
16	0.16 (0.04)	89	563 (126)	0.53 (0.06)	52	98 (11)
17	0.18 (0.11)	17	97 (63)	0	0	0
19	0.18 (0.11)	6	34 (22)	0	0	0
21	0.07 (0.02)	205	2944 (671)	0.06 (0.02)	55	978 (286)
22	0.22 (0.05)	45	202 (48)	0.02 (0.02)	5	245 (249)
23	0.17 (0.04)	63	378 (90)	0.18 (0.04)	41	224 (55)
27	0.21 (0.04)	108	516 (95)	0.12 (0.03)	40	327 (83)
29	0.07 (0.07)	23	331 (320)	N/A	7	N/A
31	0.29 (0.12)	16	54 (23)	0.13 (0.08)	5	38 (22)
32	0.11 (0.10)	9	86 (81)	N/A	1	N/A
35	0.17 (0.11)	8	46 (30)	0	0	0
36	0.09 (0.04)	50	555 (217)	0	0	0
38	0.29 (0.14)	7	24 (12)	0.33 (0.10)	12	37 (11)
42	0.21 (0.11)	11	52 (27)	0.07 (0.08)	2	27 (28)

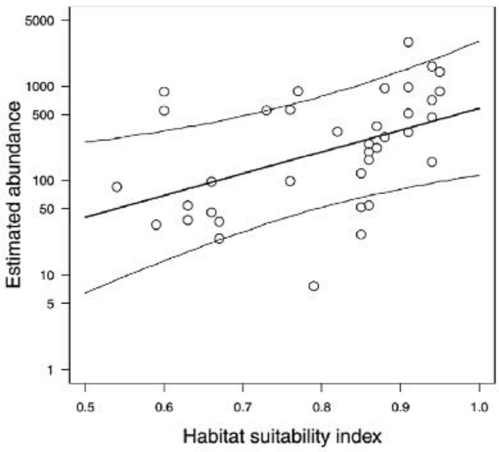

Fig. 2. The relationship between HSI and abundance. A symbol represents one pond and season (early, late) combination. The thick line is the regression and the thin lines are the 95% confidence limits. The *y*-axis is logarithmic. We used the sim() function in the package "arm" (Gelman et al. 2015) to predict and plot regression lines and confidence intervals.

We computed model averaged parameter estimates (Burnham & Anderson 2002). Model averaged daily survival probability was 0.98 ± 0.002. Model averaged detection probabilities ranged from 0.02 ± 0.01 to 0.53 ± 0.06 for the 23 ponds (Table 2). Since four detection parameters were inestimable because of a low number of recaptures and because five ponds dried out at the end of the season, we calculated population size for 22 ponds in the early capture session and for 15 ponds in the late capture session. The estimated population size of Great Crested Newts ranged from about 7 to almost 3000 individuals in the observed water bodies (Table 2).

Habitat suitability, population size, and body condition

At the level of the ponds, the analysis revealed a positive relationship between the logarithm of population size and standardized HSI ($\log(N_i) = 1.049 + 5.318\ \mathrm{HSI}_i$ (where i is for pond i); 95% confidence intervals for intercept and slope were (−2.26, 4.36) and (1.15, 9.47), respectively; Fig. 2).

At the level of individuals, only population size and capture session had 95% confidence intervals that did not overlap with zero (Table 3). For all three body condition indices, higher population size leads to lower body condition (Fig. 3) and newts displayed lower body condition later in the season. 95% confidence intervals of all other factors included zero. In the case of HSI and reproductive status the direction of effect was sometimes positive and sometimes negative for the three different body condition indices (Table 3).

Table 3. Results of mixed model analyses relating three body condition indices to abundance, capture session, HSI, reproduction and sex. Pond identity was used as a random effect. *N*, estimated abundance. *Seas*, capture session (early (April/May) or late (June/July) in the season). *HSI*, habitat suitability index. *Repr*, reproductive status of the population. *Sex*, sex of the individual. *K*, Fulton's index. R_i, residual condition index. W_r, relative mass condition index.

Variable	*K*		R_i		W_r	
	Coefficient	(95% CI)	Coefficient	(95% CI)	Coefficient	(95% CI)
N	−0.090	(−0.140, −0.036)	−0.013	(−0.022, −0.004)	−1.502	(−2.474, −0.448)
Seas	−0.087	(−0.148, −0.024)	−0.016	(−0.026, −0.006)	−1.782	(−2.946, −0.563)
HSI	0.234	(−0.215, 0.683)	−0.037	(−0.040, 0.116)	3.958	(−5.000, 12.909)
Repr	0.060	(−0.061, 0.180)	−0.009	(−0.011, 0.031)	1.293	(−1.107, 3.686)
Sex	0.108	(0.072, 0.145)	0.002	(−0.003, 0.008)	0.277	(−0.417, 0.972)

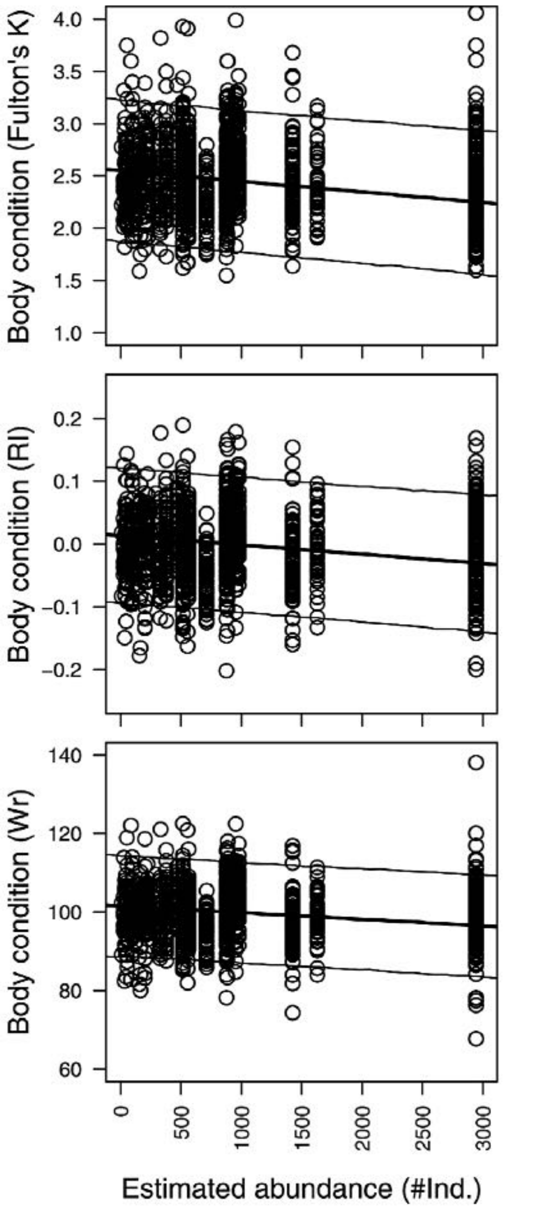

Fig. 3. The relationship between abundance and body condition. Each dot is an individual. The lines are the regression and the thin line is the 95% confidence limits. We used the sim() function in the package "arm" (Gelman et al. 2015) to predict and plot regression lines and confidence intervals.

Discussion

In the examined metapopulation of pond-breeding Great Crested Newts, habitat suitability was positively associated with population size but there was no association with body condition. There was a negative association between body condition and population size, however (Figs. 2 and 3), possibly as a consequence of intraspecific competition for resources. The HSI was originally shown to predict newt population size (i.e., counts; Oldham et al. 2000) and many phenotypic traits of individuals vary with population size and density (White et al. 2007). Research on other systems showed that relationships between habitat suitability and individual performance were weak and depended on species and phenotypic traits (Thuiller et al. 2010). Other studies revealed contrasting effects of habitat suitability on different metrics that were used to evaluate organismal performance (Whitman & Ackerman 2015) and still others found that the relationships were scale-dependent (Bean et al. 2014). Ousterhout et al. (2015) even argued that body size and population size should not be used to describe habitat suitability. Thus, our results indicate that the effect of habitat suitability (or quality) is not straightforward; population parameters, such as population size, and phenotypic traits of individuals, such as body condition, can provide quite different answers.

In the Great Crested Newt, Oldham et al. (2000) reported an effect of HSI on population size. Later, Unglaub et al. (2015) demonstrated for the same species, that HSI did not predict species occurrence or individual survival, but rather predicted where newts reproduced. Here, we further corroborate the effect of HSI on population size but in contrast to Oldham et al. (2000) our data account for imperfect detection (Fig. 2). Furthermore, we show an effect of HSI on body condition—indirectly, as body condition was negatively correlated with population size. Being aware that there are many more factors which may affect the population dynamics of newts (Cayuela et al. 2017; Griffiths, Sewell, & McCrea 2010), we posit that the model for population dynamics proposed by Solberg, Sæther, Strand, and Loison (1999) may also apply to newts. Solberg et al. (1999) showed a density-dependent decrease in female body condition which led to an inverse relationship between recruitment rate and population density. They suggested that this might be the mechanism which regulated population dynamics. Lower body condition may lead to reduced fecundity in amphibians (Reading & Clarke 1995). Consequently, a population size-dependent decrease in body condition may be a regulatory mechanism in the dynamics of the population. This conjecture is supported by matrix models suggesting that Crested Newt populations are very sensitive to changes in fecundity (Karlsson, Betzholtz, & Malmgren 2007). Newts have a relatively low annual survival probability of approximately 50% (Cayuela et al. 2017; Griffiths et al. 2010; Halley, Oldham, & Arntzen 1996), hence one may generally expect that population growth is sensitive to variation in fecundity and recruitment (Schmidt, Feldmann, & Schaub 2005).

In most species distribution models, habitat suitability is relative rather than absolute, because species prevalence cannot be estimated from presence-only data (Guillera-Arroita et al. 2015; Hastie & Fithian 2013), i.e., if $y = \alpha + \beta * x$ describes the relationship between species occurrence, y, and the habitat, x, then one can estimate only the coefficient β, whereas α cannot be estimated (Cruickshank, Ozgul, Zumbach, & Schmidt 2016). Since the absolute magnitude of suitability is unknown (i.e., α is unknown), we believe that it is necessary to quantify the strength of the relationship between habitat suitability (based on environmental characteristics) and the performance of individuals and populations (Van Horne 1983; Johnson 2007). As Schmidt and Pellet (2005) and Yackulic, Nichols, Reid, and Der (2015) suggested, dynamic measures of performance such as demography and population turnover may be better than static ones. Recently, population growth was used as a metric for habitat suitability (Hooper et al. 2008). This type of modelling might be improved through the use of integral projection models. This class of models can directly link phenotypic traits of individuals, population growth rate, and environmental conditions (Ozgul et al. 2010; Woodworth, Wheelwright, Newman, Schaub, & Norris 2017). Population dynamic models might serve as a mechanistic description of the niche of a species (Kearney 2006) and lead to a deeper understanding of the relationships between demography, habitat, environment, and the niche.

Conflict of interests

None.

Authors' contributions

BRS and SS conceived and designed the study. BU conducted the field work. BU, DK and BRS performed the statistical analysis. BU and BRS wrote the manuscript with help from SS and AH.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.01.002.

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Appendix A. Supplementary data

Table S1. Parameter estimates (on the logit scale) of the four top-ranking Cormack Jolly Seber models estimating apparent survival Φ of Great Crested Newts.

Model	Beta	Estimate	95% CI
logit (Φ) = β_0	β_0	4.02	3.79 – 4.26
logit (Φ) = $\beta_0 + \beta_1$ x K	β_0	4.40	2.96 – 5.84
	β_1	-0.15	-0.72 – 0.42
logit (Φ) = $\beta_0 + \beta_1$ x R_i	β_0	4.02	3.79 – 4.26
	β_1	-0.67	-4.26 – 2.92
logit (Φ) = $\beta_0 + \beta_1$ x W_r	β_0	4.59	1.42 – 7.77
	β_1	-0.01	-0.04 – 0.03

Φ: survival probability. K: Fulton's index. W_r: relative mass condition index. R_i: residual condition index. CI: confidence interval.

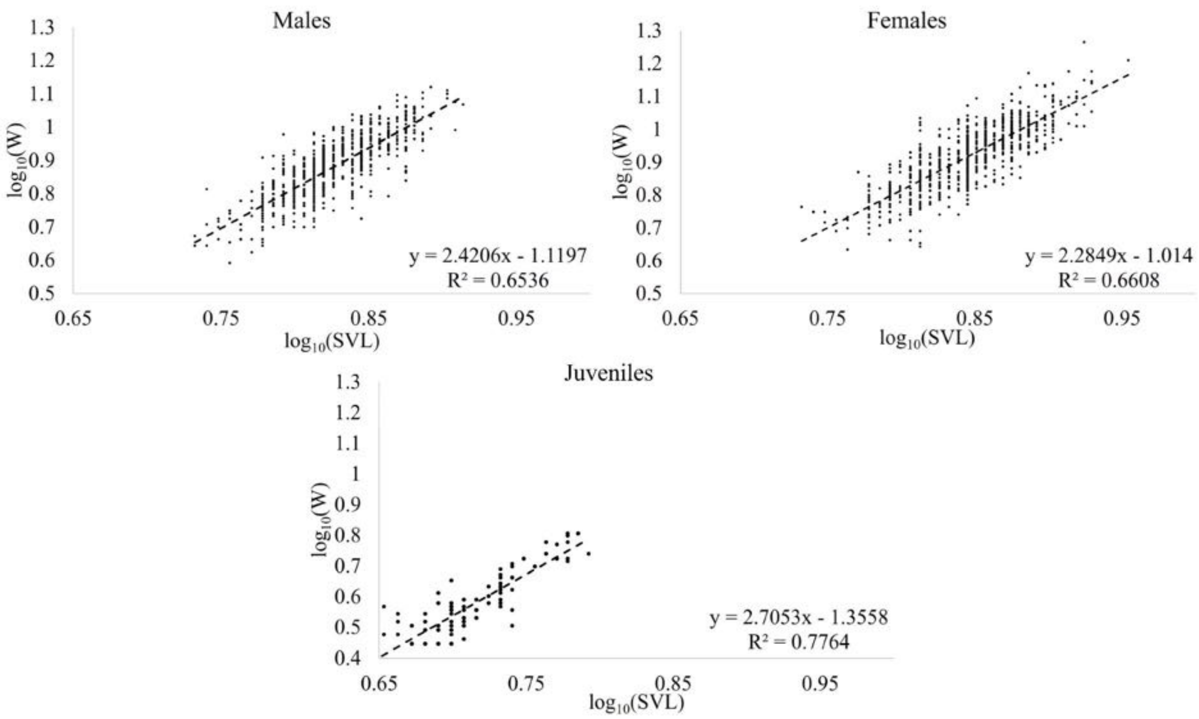

Fig. S1. Relationship between $\log_{10}$-transformed body mass (W) and snout-vent length (SVL) in Great Crested Newts (*Triturus cristatus*).

Chapter III

Context-dependent dispersal determines relatedness and genetic structure in a patchy amphibian population

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Context-dependent dispersal determines relatedness and genetic structure in a patchy amphibian population

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Abstract

Dispersal is a central process in ecology and evolution with far reaching consequences for the dynamics and genetics of spatially structured populations (SSPs). Individuals can adjust their decisions to disperse according to local fitness prospects, resulting in context-dependent dispersal. By determining dispersal rate, distance and direction, these individual-level decisions further modulate the demography, relatedness and genetic structure of SSPs. Here, we examined how context-dependent dispersal influences the dynamics and genetics of a great crested newt (*Triturus cristatus*) SSP. We collected capture–recapture data of 5564 individuals and genetic data of 950 individuals across an SSP in northern Germany. We added genetic data from six sites outside this SSP to assess genetic structure and gene flow at a regional level. Dispersal rates within the SSP were high but dispersal distances were short. Dispersal was context-dependent: individuals preferentially immigrated into high-quality ponds where breeding probabilities were higher. The studied SSP behaved like a patchy population, where subpopulations at each pond were demographically interdependent. High context-dependent dispersal led to weak but significant spatial genetic structure and relatedness within the SSP. At the regional level, a strong hierarchical genetic structure with very few first-generation migrants as well as low effective dispersal rates suggest the presence of independent demographic units. Overall, our study highlights the importance of habitat quality for driving context-dependent dispersal and therefore demography and genetic structure in SSPs. Limited capacity for long-distance dispersal seems to increase genetic structure within a population and leads to demographic isolation in anthropogenic landscapes.

KEYWORDS

gene flow, habitat quality, metapopulation, patchy population, *Triturus cristatus*

Bianca Unglaub and Hugo Cayuela are shared first authorship.

1 | INTRODUCTION

Dispersal (i.e., all movements of an individual or propagule possibly leading to gene flow; Ronce, 2007) is a central process in ecology and evolution that has far reaching consequences for population dynamics, genetics and conservation (Bailey & Muths, 2019; Bowler & Benton, 2005; Legrand et al., 2017; Ronce, 2007). Dispersal is usually viewed as a three-stage process (Clobert et al., 2009) including emigration from the habitat patch (departure), transience in the landscape matrix and immigration into a new habitat patch (arrival). Phenotypic traits such as morphology, physiology and behaviour influence each stage of the dispersal process, leading to condition-dependent dispersal and dispersal syndromes (Cote et al., 2010; Ronce & Clobert, 2012). Furthermore, individuals use social and environmental cues to adjust their emigration and immigration decisions to maximize their fitness within a patch (i.e., "context-dependent dispersal" or "informed dispersal"; Clobert et al., 2009). In particular, habitat quality and social factors such as inbreeding risk, kin competition and conspecific density may affect the decision of an individual to stay or to move from its patch (Bowler & Benton, 2005; Matthysen, 2012). In addition, the Euclidean distance between patches and the composition of the landscape matrix strongly affect the capacity of individuals to disperse (Baguette et al., 2013). Understanding how the complex interplay between individual phenotypes, patch-specific factors and landscape determines dispersal patterns is a critical step to understand and predict population dynamics and genetic structure.

Dispersal plays a central role in the dynamics of spatially structured populations (SSPs), which are composed of a set of subpopulations occupying discrete breeding patches that are connected by dispersing individuals and regulated by local demographic processes (i.e., mortality and natality; Thomas & Kunin, 1999). By affecting the intensity and direction of individual movement between patches, dispersal strongly influences the structure and growth rate of subpopulations via emigration and immigration, and ultimately the long-term persistence of the whole SSP (Bowler & Benton, 2005; Hanski & Gaggiotti, 2004). For this reason, dispersal has tremendous importance in the classification of the different types of SSP (i.e., Levins-type metapopulation, patchy population and source–sink systems), which can be positioned along a gradient of dispersal intensity (Ovaskainen & Hanski, 2004). At one end of the gradient, an SSP can behave as a patchy population (Harrison, 1991), where individuals disperse frequently among patches and reproduce in several patches during their lifetime. In this type of SSP, dispersal is so high that the system is effectively a single demographic unit which is unlikely to go extinct (Harrison, 1991). At the other end, SSPs show the characteristics of the classic Levins-type metapopulation (Hanski, 1999; Levins, 1969), where most individuals remain in their natal patch, and dispersal events among subpopulations are infrequent, although the dispersal rate is high enough to allow eventual recolonization of patches where a subpopulation has gone extinct. Furthermore, the nonrandomness and asymmetry of dispersal is another essential aspect for SSP classification (Ovaskainen & Hanski, 2004; Thomas & Kunin, 1999). In source–sink and pseudo-sink systems, individuals from productive high-quality patches move to low-quality patches where local reproductive success fails to balance local mortality, thereby allowing the long-term persistence of subpopulations in low-quality patches (Kawecki, 2004; Pulliam, 1988; Runge et al., 2006). While true sinks would not be viable without immigration from source populations, high immigration rates into pseudo-sinks increase the local population size above the carrying capacity of the patch and consequently depress local reproductive success or increase local mortality as a result of density-dependence. In these systems, the persistence of the SSP depends on the existence of one or more source populations, while extinction–colonization dynamics depend on habitat quality. Although theoretical models describing those population systems were proposed long ago, the empirical testing of their assumptions is still limited to a small number of taxa, mainly due to the scarcity of longitudinal demographic data collected across large SSPs.

Since successful reproduction of dispersing individuals leads to gene flow, dispersal has a strong influence on the genetic structure and connectivity within an SSP (Broquet & Petit, 2009; Cayuela, Rougemont, et al., 2018; Lowe & Allendorf, 2010). As dispersal intensity and nonrandomness strongly determine the classification of SSPs, one might expect contrasting genetic and relatedness structure in Levins-type metapopulations, patchy populations, and source–sink systems (Gaggiotti, 1996; Hastings & Harrison, 1994). In an SSP that behaves like a Levins-type metapopulation, a low dispersal rate should lead to a low effective dispersal rate (or "migration rate"; Broquet & Petit, 2009; Cayuela, Rougemont, et al., 2018) and strong genetic differentiation between patches is evident, expressed as marked isolation-by-distance (IBD) patterns. Low levels of gene flow should also lead to a decrease of genetic variation and a small effective population size (N_e). In addition, individuals in a specific patch should show high levels of relatedness and high inbreeding coefficients. By contrast, an SSP behaving as a patchy population should present the reverse characteristics, due to high dispersal rate and subsequent gene flow. In an SSP following the source–sink model, genetic structure is expected to be weak due to continuous gene flow between source and sink subpopulations driven by habitat quality (Gaggiotti, 1996). In particular, effective dispersal rates are likely to be asymmetric due to nonrandom dispersal; dispersal should mainly occur from source (high-quality patches) to sink (low-quality patches) subpopulations. As a consequence, observed genetic substructure and IBD should be weak, and relatedness and inbreeding coefficients—as well as N_e—should be habitat-dependent.

Pond-breeding amphibians are excellent models to study the influence of dispersal on the dynamics of SSPs and their genetic structure (Cayuela, Valenzuela-Sánchez, et al., 2020; Marsh & Trenham, 2001; Smith & Green, 2005). First, populations of pond-breeding amphibians follow the typical structure of SSPs: breeding subpopulations occupy discrete aquatic patches (e.g., ponds, lakes) connected by dispersing individuals (Cayuela, Valenzuela-Sánchez, et al., 2020). Second, dispersal rates and distances vary strongly both within and between species (Cayuela, Valenzuela-Sánchez, et al., 2020); this determines the position of an SSP along the gradient from a Levins-type metapopulation to patchy population (Smith & Green, 2005) and strongly influences its long-term viability (Cayuela, Besnard, et al., 2020). Although amphibian SSPs were initially considered to constitute Levins-type metapopulations, increasing evidence suggests that many amphibian SSPs instead behave like patchy populations (Cayuela, Besnard, et al., 2020; Smith & Green, 2005). Furthermore, although simulation models and empirical data suggest that source–sink systems might exist in amphibians (Gill, 1978; Sinsch, 1992; Sjögren Gulve, 1994; Willson & Hopkins, 2013), the assumption of this model has rarely been empirically tested due to the lack of fine-scale demographic data collected in an amphibian SSP. Third, dispersal can be context-dependent in amphibians, suggesting that individuals adjust their emigration and immigration decisions according to conspecific and heterospecific density (Cayuela et al., 2018, 2019), and environmental factors that affect local breeding success (Boualit et al., 2019). Amphibians actively search for breeding ponds using acoustic, magnetic, visual and olfactory cues for both short- and long-distance orientation (Joly, 2019; Sinsch, 2006, 2014). In particular, amphibians use olfaction to orient toward their breeding pond at distances 100–300 m away from it, identify their natal pond and select their oviposition site (Joly, 2019; Jørgensen, 2000; Ogurtsov, 2004; Sinsch, 2006). Such behavioural processes result in nonrandom dispersal rates and distances in SSPs, drastically affecting gene flow (Berven & Grudzien, 1990; Cayuela, Besnard, et al., 2020; Funk et al., 2005), relatedness and inbreeding within breeding patches, as well as N_e (Cayuela, Besnard, et al., 2020).

Here, we examine how dispersal influences the dynamics and genetic structure of an SSP of the great crested newt (*Triturus cristatus*), a pond-breeding amphibian of European conservation concern. Based on an extensive capture–recapture data set of 5564 marked individuals across a large SSP (33 ponds in an area of 7.7 km^2, of which 27 ponds held breeding subpopulations), we assessed whether the studied SSP behaves like a Levins-type metapopulation, a patchy population or a source–sink system. We quantified the proportion of dispersing individuals and fitted dispersal kernels (these quantify the relationship between dispersal event frequency and Euclidean distance). Furthermore, we empirically tested the assumption of the source–sink model. Under this model, we expected that adult survival and/or breeding probability are positively correlated with habitat quality, and that individuals from high-quality ponds immigrate to low-quality ponds. Alternatively, under the hypothesis of "informed dispersal" (Clobert et al., 2009), we expected that individuals are less likely to emigrate from high-quality ponds and preferentially immigrate to high-quality ponds. In addition, we verified that pond quality was an accurate predictor for the occurrence of reproduction using multistate occupancy models that took pond connectivity within the SSP into account. Furthermore, we examined the genetic structure of the SSP using 1266 individuals genotyped for 17 microsatellite loci. Under a patchy population model with intense gene flow, genetic structure and IBD patterns should be weakly expressed. Furthermore, we expected low relatedness levels within ponds and low variation in inbreeding and relatedness across ponds. Finally, we assessed genetic structure and gene flow at a regional level within an area of about 350 km^2. We expected that populations separated by Euclidean distances exceeding the distance covered during long-distance dispersal events should behave like independent demographic units. We investigated this hypothesis by analysing hierarchical genetic structure and quantifying (molecular) migration rates between the different genetic clusters.

2 | MATERIALS AND METHODS

2.1 | Study species and study sites for demographic and genetic analyses

Triturus cristatus is a widely distributed European pond-breeding amphibian. Adult newts can be found in ponds during the breeding season which begins in February/March and ends in June/July (Jehle et al., 2011). Their ventral colour pattern is highly variable and unique, allowing visual individual recognition in capture–mark–recapture studies (Drechsler et al., 2015). Drechsler et al. (2013) characterized 17 polymorphic microsatellite loci for the analysis of genetic population structure. While the maximum dispersal of a single individual within 1 year was recorded as 1290 m in an anthropogenic landscape (Kupfer, 1998), the habitat used during the terrestrial phase is usually close to the breeding pond (less than 150 m away from the pond; Jehle & Arntzen, 2000). More details about the biology and conservation status of the species are given in the extended methods section of the Supporting Information.

We analysed dispersal and gene flow in an SSP encompassing 33 ponds that are located in two adjacent nature reserves called "Höltigbaum" and "Stellmoorer Tunneltal," covering an area of ~7.7 km^2. At the regional scale (350 km^2), we analysed genetic structure of crested newt populations by adding six additional sampling sites distributed in the surroundings of Hamburg, Germany (Figure 1; see Supporting Information for a detailed description of these sites). The maximum distance between sampling sites at the regional scale is 27 km along the north–south axis, and 13 km along the east–west axis.

2.2 | Demographic analyses within the SSP

2.2.1 | Capture–recapture survey and data

We collected capture–recapture data between 2012 and 2014 across 33 waterbodies within the area of the SSP (Figure 2; site 1 in Figure 1). Newts were captured using Ortmann's funnel traps (Drechsler et al., 2010) during two capture sessions (*cs*) per year, one early (April/May) and one late (June/July) in the breeding season. Every capture session consisted of three consecutive capture events every 2 days (see Supporting Information for more details on collection of data).

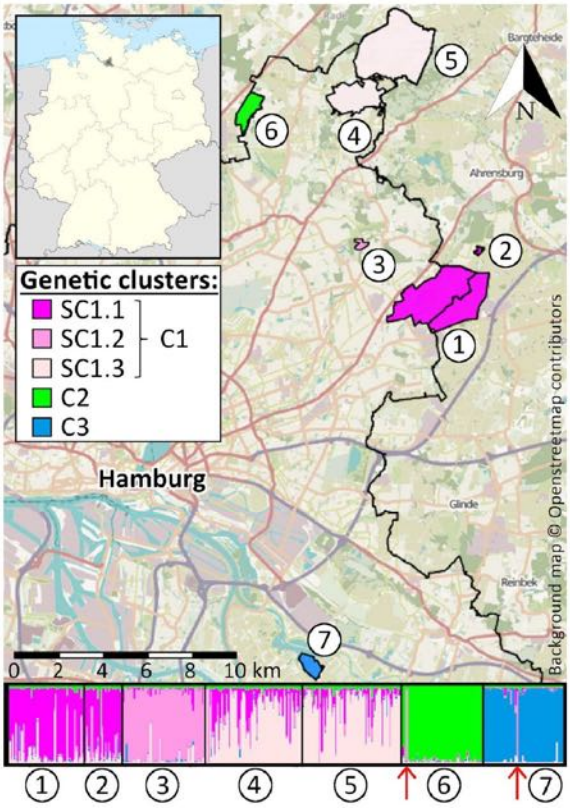


FIGURE 1 Locations of the seven sampling sites in the area of Hamburg, Germany (i.e., the regional level). Genetic clustering analyses of the program STRUCTURE resulted in three different clusters (C1, C2 and C3; $k = 3$, indicated by different colours: pink, green and blue) and three different genetic subclusters (SC1.1, SC1.2 and SC1.3) within cluster C1 ($k = 5$, indicated by different pink shades). Red arrows indicate two possible F_0 migrants

2.2.2 | Estimating dispersal distances

We used multistate mark–recapture models (Lebreton et al., 2009) implemented in the program MARK (version 6.2; White & Burnham, 1999) to estimate dispersal distances. Model notation follows the standard notation of Lebreton et al. (1992). The model allows estimation of three parameters: apparent survival (Φ), detection probabilities (p) and dispersal probability (Ψ). In this analysis, apparent survival (Φ) was modelled as constant (.). Detection probabilities (p) were modelled as either constant (.), or as varying among different ponds (Pond), among different years (Y) or the additive effect thereof (Pond + Y). Dispersal probability (Ψ) was modelled as constant (.) or as a function of distance between ponds (Dist). This resulted in a set of eight candidate models (see Table 1). Capture events were pooled for early and late capture sessions within each year. We accounted for the unequal time intervals among *cs* (6–8 weeks among *cs* within the same year and 37–40 weeks among *cs* of different years) and estimated weekly survival and dispersal probabilities. Annual apparent survival was calculated as $(\Phi)^{52}$. The corresponding standard error was calculated by applying the delta method (Seber, 1982), and 95% confidence intervals (CI) were obtained using the formula 95% CI = estimate ± 1.96 × *SE*. Model selection was based on the Akaike information criterion adjusted for small sample size (AICc; Burnham & Anderson, 2002). Akaike weights (w) were used as a measure of relative support for each model.

2.2.3 | Estimating the proportion of dispersing individuals

We used the multi-event capture–recapture model described in Denoël et al. (2018) to estimate the proportion of individuals with a dispersing phenotype (i.e., individuals that have dispersed at least once during the study period) within the SSP. In this model, two discrete classes of individuals are considered to accommodate heterogeneity of demographic parameters (Péron et al., 2010; Pradel, 2009). The model includes four main parameters which are estimated from the data: (r) the proportion of individuals with a non-dispersing phenotype, and ($1 - r$) the proportion of individuals with a dispersing phenotype; (Φ) the probability of apparent survival; (α) the probability that an individual with a dispersing phenotype remains in the same pond between two sampling sessions (intra-annual: from April/May to June/July; inter-annual: from June/July to April/May), and ($1 - \alpha$) the probability that it moves to another pond; and (p) recapture probability. For one of the heterogeneity classes, the probability that individuals remained at the same pond is fixed at $\alpha = 1$, which allows for identification of individuals with a non-dispersing phenotype (Cayuela, Boualit, et al., 2019; Denoël et al., 2018). The model was implemented in the program E-SURGE (Choquet et al., 2009). All parameters of the model were kept constant, except for recapture probability which differed among years.

2.2.4 | Evaluating the effect of habitat quality on survival, emigration and immigration

Habitat quality was evaluated using the standard habitat suitability index (HSI) developed for *T. cristatus* (Oldham et al., 2000). The HSI ranges from 0 (unsuitable habitat) to 1 (best habitat) and is based on 10 habitat features (e.g., pond area, pond permanence, water quality, fish presence) that can easily be measured in the field or derived from digital maps (see Unglaub et al., 2015). According to the HSI, the optimal habitat for *T. cristatus* would be a temporary, fish-free pond of about 600 m^2 in size, which has good water quality and a diverse macrophyte cover, and which is situated in the centre of the species distribution range, highly connected to other ponds and surrounded by suitable terrestrial habitat where newts can find shelter outside the reproductive season. Newts are more abundant in ponds with a high HSI (Unglaub et al., 2018).

The influence of the HSI on survival, emigration and immigration was examined using the multi-event capture–recapture model

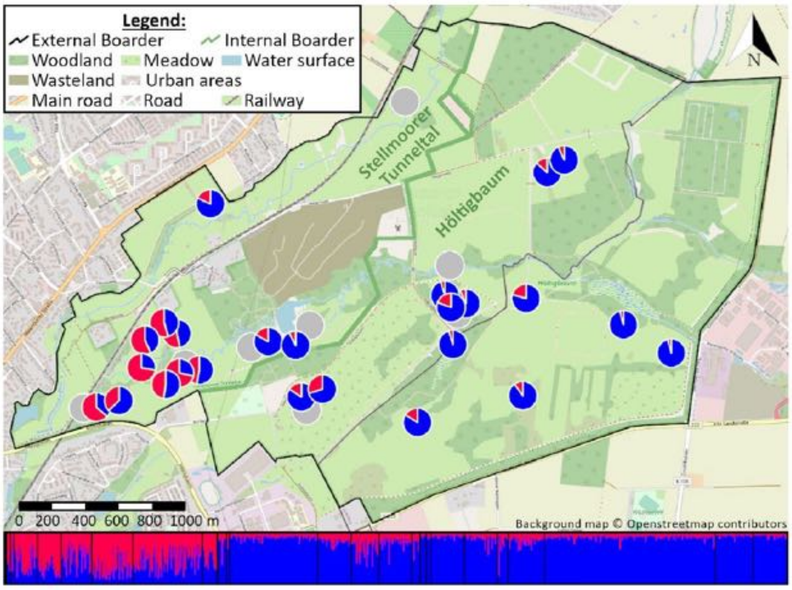


FIGURE 2 Locations of the 33 surveyed ponds within the spatially structured population. Genetic clustering analysis using STRUCTURE resulted in two different genetic population units ($k = 2$): the northeastern (NE; blue) and the southwestern (SW; red) demes. Ponds where no genetic samples were collected (i.e., which were not occupied in 2012) are shown in grey

TABLE 1 Selection of multistate mark–recapture models for estimating apparent survival and dispersal probabilities of *Triturus cristatus* within the spatially structured population

Model	ΔAICc	w	k
φ (.), p (Pond), Ψ (Dist)	0	0.8080	30
φ (.), p (Pond + Y), Ψ (Dist)	2.87	0.1920	32
φ (.), p (Y), Ψ (Dist)	303.34	0	6
φ (.), p (.), Ψ (Dist)	304.35	0	4
φ (.), p (Pond), Ψ (.)	741.08	0	29
φ (.), p (Pond + Y), Ψ (.)	743.54	0	31
φ (.), p (Y), Ψ (.)	1001.62	0	5
φ (.), p (.), Ψ (.)	1002.49	0	3

AICc of the best model was 9038.35. Survival probability (Φ) was modelled as constant (.). Capture probability p was modelled as constant (.), and as varying among ponds (Pond), among years (Y) or the additive effect thereof (Pond + Y). Dispersal probability (Ψ) was modelled as constant (.) or as a function of distance between ponds (Dist). AICc: corrected Akaike's information criterion; ΔAICc: difference of the AICc value of the model with the lowest AICc score and the given model; w: Akaike weight; k: number of parameters.

proposed by Tournier et al. (2017), which is an adaptation of the model proposed by Cayuela et al. (2017). The model allows estimation of four parameters of interest: apparent survival probability (φ), emigration probability (ε), immigration probability (α) and recapture probability (p). The model was implemented in the program E-SURGE. Candidate models were ranked through a model-selection procedure using AICc and Akaike weights (w) (Burnham & Anderson, 2002). We performed model-averaging when w of the best-supported model was lower than 0.90. We considered both intra- and inter-annual emigration and immigration probability. To simplify the model structure, intra-annual survival was fixed at $\varphi = 1$, meaning that we only modelled inter-annual survival. Ponds were classified as either high-HSI ponds when HSI ≥ 0.78 or low-HSI ponds when HSI < 0.78; the mean HSI across all ponds was 0.78. In our modelling system, individuals can emigrate from the pond they occupy depending on its HSI status (high-HSI or low-HSI pond). Individuals that have emigrated can then immigrate in a pond with high or low HSI. The effect of HSI on survival, emigration and immigration was examined from the following model: {φ (HSI), ε (HSI), α (HSI), p (HSI + Y)}; where Y was the year-specific effect included in recapture probability. We tested all combinations of effects leading to 16 candidate models (see Table 2).

2.2.5 | Evaluating the effect of habitat quality on occurrence of reproduction

We investigated the effect of HSI on adult occurrence and breeding probabilities while taking connectivity among ponds into account. We recorded the presence or absence of newts as well as the occurrence of larvae within 33 ponds of the SSP. Ponds were surveyed during a third capture session in late July/early August in order to detect the presence of larvae. We used the detection/nondetection of larvae as a proxy for successful reproduction (we adjusted for imperfect detection; see below). Adult newts were captured in 27 of 33 surveyed ponds. In the remaining six ponds, no newts were detected in any year of the survey. Larvae were detected in only 19 of 27 occupied ponds. While occupancy states (i.e., whether the species is either present or absent) did not change during the 3 years of sampling (except for one pond which dried up in 2012), the reproduction state (i.e., whether larvae are either present or absent) differed among years. In order to model both the presence/absence of newts and the presence/absence of reproduction (given occurrence), we used a multiseason multistate occupancy model (MacKenzie et al., 2009). This model assumes that the true latent state of the ponds falls into one of three categories: (0) absence of

TABLE 2 Testing the effect of pond quality on adult survival, emigration and immigration

Model	k	Deviance	AICc	w
φ (.), ε (.), α (HSI), p (Y)	10	13,713.70	13,733.74	0.30
φ (HSI), ε (.), α (HSI), p (Y)	11	13,712.84	13,734.88	0.17
φ (.), ε (HSI), α (HSI), p (Y)	11	13,713.16	13,735.20	0.14
φ (.), ε(.), α (HSI), p (HSI + Y)	11	13,713.68	13,735.72	0.11
φ (HSI), ε (.), α (HSI), p (HSI + Y)	12	13,711.91	13,735.95	0.10
φ (HSI), ε (HSI), α (HSI), p (Y)	12	13,712.22	13,736.26	0.08
φ (.), ε (HSI), α (HSI), p (HSI + Y)	12	13,713.16	13,737.21	0.05
φ (HSI), ε (HSI), α (HSI), p (HSI + Y)	13	13,711.54	13,737.60	0.04
φ (HSI), ε (.), α (HSI), p (HSI)	10	13,799.05	13,819.09	0.00
φ (.), ε (.), α (HSI), p (.)	8	13,803.09	13,819.11	0.00
φ (.), ε (.), α (HSI), p (HSI)	9	13,801.56	13,819.59	0.00
φ (.), ε (HSI), α (HSI), p (HSI)	9	13,802.55	13,820.58	0.00
φ (HSI), ε (.), α (HSI), p (.)	9	13,802.87	13,820.90	0.00
φ (HSI), ε (HSI), α (HSI), p (HSI)	11	13,798.93	13,820.97	0.00
φ (.), ε (HSI), α (HSI), p (.)	10	13,801.34	13,821.37	0.00
φ (HSI), ε (HSI), α (HSI), p (.)	10	13,802.29	13,822.32	0.00

Survival probability (φ), emigration probability (ε), immigration probability (α) and recapture probability (p) were modelled as constant (.) or as a function of the habitat suitability index (HSI). Recapture probability was also modelled as varying among years (Y). *k*: number of model parameters; Deviance: residual deviance; AICc: Akaike information criterion adjusted for small sample size; *w*: Akaike weight.

the species, (1) presence without reproduction or (2) presence with reproduction (i.e., presence of larvae). We used only data gathered during the second and third capture session each year for this part of the analyses because larvae were only present during these capture sessions.

We tested whether pond occupancy (ψ) and reproduction probabilities (R) are influenced by HSI, pond surface area and connectivity using the program PRESENCE (version 10.2; Hines, 2006) and used AIC for model selection (Burnham & Anderson, 2002). Connectivity was calculated according to the formula of the incidence function model (Hanski, 1999): $S_i = \Sigma_{j \neq i} \exp(-\alpha d_{ij}) A_j$, where $\alpha = 1$/average dispersal distance (the average dispersal distance observed in this study using mark–recapture methods was 137 m), d_{ij} = distance between pond i and pond j, and A_j = area of pond j.

We used a two-step approach to model selection as commonly done in site occupancy analyses (e.g., Groff et al., 2017; Valdez et al., 2015; Weir et al., 2005) and that does not lead to biased parameter estimates in mark–recapture modelling (Doherty et al., 2012). We first modelled the detection process and then the probabilities of site occupancy and reproduction. To identify the best detection model, we held occupancy parameters (ψ and R) constant and evaluated the effect of capture session (*cs*) and sampling year (Y), as well as the interaction of both on detection probabilities: (1) the probability of detecting occupancy given that a pond was occupied without reproduction (p^1), (2) the probability of detecting occupancy given that a pond was occupied with successful reproduction (p^2) and (3) the probability of correctly identifying a pond as a breeding site given that successful reproduction did occur (δ). We then analysed the effects of connectivity (S), pond surface area (Area) and habitat quality (HSI) on pond occupancy (ψ) and reproduction probability (R), while using the best detection model as determined in the first step. Since we observed a single extinction event when a pond dried completely in 2012, we were mainly interested in the influence of these explanatory variables on occupancy and reproduction probabilities rather than in state transition probabilities between years. Variables describing changes over time (i.e., ψ^m_{t+1} and R^m_{t+1} in the transition probability matrix, where m = state) were therefore modelled in the same way as the initial variables (i.e., ψ_{t-1} and R_{t-1}; see MacKenzie et al., 2009; Unglaub et al., 2015).

2.3 | Genetic analyses

2.3.1 | DNA extraction and microsatellite loci genotyping

In total, 1266 tissue samples were taken from the SSP and the six additional sites (Tables S1a and S1b) by puncturing the tails of newts using micro haematocrit capillary tubes (Carl Roth, Ø 1.6 mm). Tissue samples were stored in 80% ethanol. Within the SSP, 950 samples were collected at 25 ponds (Table S1b). To explore structuring at the regional level, we included 316 samples from six additional sites (sites 2–7; 25–66 samples per site). To avoid overrepresentation of individual genotypes from the SSP, we used a standardized sample of 50 representative individual genotypes by random pruning following Chikhi et al. (2010). Taken together, this resulted in a total of 366 genetic samples for the regional scale including samples from both within and outside the SSP (Table S1a). Each individual sample was genotyped for 17 microsatellite loci (see Drechsler et al., 2013 and Supporting Information for more details).

2.4 | Genetic analyses within the SSP

2.4.1 | Genetic diversity estimates

Across the SSP, 950 individuals could be genotyped for 17 microsatellite loci. Individuals with more than 50% of loci missing (nine individuals) were discarded from further analysis. We computed exact tests (10,000 dememorization steps; 100,000 Markov chain Monte Carlo [MCMC] chain length) for each locus per site to test for significant deviations from Hardy–Weinberg equilibrium (HWE, after Bonferroni correction $p < .002$) and also tested for nonrandom association of alleles at different loci (linkage disequilibrium) using ARLEQUIN 3.5.2.2. Additionally, we checked for the presence of null alleles, scoring errors and large allele dropouts in MICROCHECKER (Van Oosterhout et al., 2004). We calculated genetic diversity parameters (allelic richness [A_r, rarefaction], observed (H_O) and expected (H_E) heterozygosity, inbreeding coefficient [F_{IS}], private alleles [P_A]) for each pond using the R packages *diveRsity* (Keenan et al., 2013) and *PopGenReport* (Adamack & Gruber, 2014).

2.4.2 | Population genetic structure analyses

To analyse the genetic population structure within the SSP, we first calculated pairwise F_{ST} values between the different ponds using the software ARLEQUIN 3.5 (Excoffier & Lischer, 2010). Only ponds with at least 20 genotyped individuals were considered. Then, we used the model-based Bayesian clustering method of the software STRUCTURE (version 2.3.4; Pritchard et al., 2000). Genotyped individuals were assigned to a number of *k* genetic clusters, using the admixture model with a local prior and a burn-in period of 20,000 MCMC generations, followed by 50,000 iterations for $k = 1$ to $k = 10$ with 10 replicates for each *k*. We used a local prior to assist genetic clustering at the SSP level because gene flow was presumed to be high. We then used the software STRUCTURE HARVESTER (Earl, 2012) to assess the most likely number of distinct genetic clusters by the estimation of Δk (Evanno et al., 2005) and the evaluation of the logarithm of the probability of the data ($\ln P(D|K)$; Pritchard et al., 2000). The program CLUMPP (Jakobsson & Rosenberg, 2007) was used to align assignment clusters across multiple replicate runs and results were displayed graphically with the program DISTRUCT (Rosenberg, 2004).

2.4.3 | Spatial extent of effective dispersal and Mantel autocorrelogram

We performed a spatial autocorrelation analysis with a nondirectional Mantel correlogram (Smouse & Peakall, 1999) using the R-package *ecodist* to assess the spatial scale of effective dispersal. Euclidean distance classes were defined every 750 m resulting in seven binary matrices representing the membership of individual pairs to the distance class tested (with "0" for pairs of individuals belonging to the same distance class and "1" otherwise). Each binary matrix was compared to a PhiST matrix (Meirmans, 2006) using a simple Mantel test with 1000 permutations. We then plotted Mantel correlation values over distance classes, with confidence intervals determined by the random removal of 5% of populations (1000 iterations).

2.4.4 | Relatedness structure and IBD analyses

We investigated relatedness structure using the program COANCESTRY version 1.0.1.8 (Wang, 2011) and linear mixed models. We used Wang's estimator (Wang, 2002) that was highly correlated (i.e., correlation coefficient >.70; Table S2) with the estimators proposed by Li et al. (1993; *LynchLi* in COANCESTRY), Lynch and Ritland (1999; *LynchRd*), and Queller and Goodnight (1989; *QuellerGt*); the correlation was lower (.40) with the Ritland estimator (Ritland, 1996). We first investigated relatedness structure within the SSP by examining whether mean relatedness among individuals within ponds exceeded relatedness between ponds. We used linear mixed models where individual pairwise relatedness coefficient was included as the response variable (i.e., 450,775 pairwise combinations), individual location was incorporated as explanatory factors with two modalities (i.e., the individuals of the dyad occupy the same pond or two different ponds), and pond was entered as a random effect (i.e., random intercept). The models were implemented in the R package *lme4* (Bates et al., 2015) and the significance of the fixed effect was evaluated with a likelihood ratio (LR) test. We also calculated the marginal R^2 for fixed effects using the *MuMIn* package (Barton, 2009).

In addition, we examined IBD patterns using an individual-based approach relying on pairwise relatedness coefficients (reviewed by Cayuela, Rougemont, et al., 2018). To this end, we built a linear mixed model where pairwise relatedness coefficient (excluding estimates of individuals occupying the same pond, leading to the consideration of 410,348 pairwise combinations) was incorporated as the response variable, Euclidean distance between ponds as the explanatory variable (centered and scaled) and pond as a random effect (i.e., random intercept). We evaluated the significance of the fixed effect with an LR test and calculated the marginal R^2.

2.4.5 | Effective dispersal rates between genetic clusters and first-generation migrants

Effective dispersal rates (i.e., migration rates) between the two genetic clusters identified by the STRUCTURE analysis within the SSP (see Section 3) were estimated using the programs BIMR (Faubet & Gaggiotti, 2008) and BAYESASS (Wilson & Rannala, 2003).

The program BIMR includes a Bayesian assignment test algorithm to estimate the proportion of genes derived from immigrants within the last generation. This multilocus genotype approach can estimate recent gene flow and provide reliable estimates when global F_{ST} values are >0.01 and the number of loci is 10 or more (Faubet & Gaggiotti, 2008). For each analysis, we ran 10 replicates with a total of 2,020,000 iterations. For every replicate, we first ran each MCMC for 20 short pilot runs of 1000 iterations each, in which incremental values were tuned by the program in order to obtain acceptance rates between 25% and 45%. We then used a burn-in period of 10^6 iterations and a sample size of 20,000 with a thinning interval of 50 iterations for each run. Following Faubet et al. (2007), we chose the run with the lowest assignment component of total deviance (D_{assign}) to extract parameter estimates. We examined the 95% highest posterior density interval (HPDI) to assess the significance of asymmetry for pair-wise dispersal rate estimates.

The program BAYESASS also uses individual multilocus genotypes to estimate recent effective dispersal rate among populations. This Bayesian approach relies on MCMC techniques to carry out the estimation of posterior probabilities. Following the developer's recommendations, we used the following program settings: the number of iterations for the MCMC was 5,000,000, the thinning interval was 5000 and the length of the burn-in period was 500,000.

To identify possible first-generation (F_0) migrants (i.e., dispersers) among the genetic clusters and to assign them to their source population, we used the Bayesian assignment procedure of Rannala and Mountain (1997), as implemented in the program GENECLASS 2.0 (Piry et al., 2004). Assignment probabilities were calculated using the Monte Carlo resampling algorithm of Paetkau et al. (2004) with 1000 simulated individuals and a threshold probability of p = .01. Since it is possible that some potential source populations were not sampled, we used L_{home} as the likelihood computation instead of L_{home}/L_{max} (Paetkau et al., 2004; Piry et al., 2004).

2.5 | Genetic analyses at the regional level

2.5.1 | Genetic diversity estimates

At the regional level, 366 individuals were genotyped for 17 microsatellite loci. The calculation of genetic population diversity estimates at the regional level followed the same workflow as at the local level within the SSP.

2.5.2 | Population genetic structure analyses

We first calculated pairwise F_{ST} values between the seven sites at the regional scale using the software ARLEQUIN 3.5. Then, we analysed the population genetic structure using the program STRUCTURE following the same approach as described above for SSP analyses. To assign all genotyped individuals to a number of k clusters, we used the admixture model without local prior (contrary to the SSP analyses) and a burn-in period of 20,000 MCMC generations, followed by 50,000 iterations for k = 1 to k = 7 with 10 replicates for each k.

2.5.3 | Spatial extent of effective dispersal and Mantel autocorrelogram

We examined the extent of effective dispersal at the regional level using a Mantel autocorrelogram, using the procedure previously described for the SSP analyses (see above) and with distance classes defined every 2 km.

2.5.4 | Effective dispersal rates between genetic clusters and first-generation migrants

Since STRUCTURE analyses revealed a hierarchical genetic population structure (see Section 3), we estimated effective dispersal rates among clusters and subclusters over a two-step approach using the programs BIMR and BAYESASS. First, we estimated effective dispersal rates among three genetic clusters (clusters 1–3; Figure 1) identified at the highest genetic structuring level. Second, at the level of cluster 1, we estimated effective dispersal rates among three distinct subclusters (subcluster 1.1–1.3; Figure 1). We tested all clusters/subclusters for F_0 migrants using the approach previously described for the SSP analyses (see above).

3 | RESULTS

3.1 | Demographic analyses within the SSP

3.1.1 | Dispersal metrics from raw capture–recapture data

In total, 5564 individual capture histories of *Triturus cristatus* (2913 males, 2651 females) were recorded within the SSP. We recaptured 917 individuals at least once, and of these, 189 (20.6%) were found in different ponds during the 3 years of our study. While 66.7% of dispersing newts changed ponds within the SW deme, 32.3% changed ponds within the NE deme, and only two individuals dispersed between demes (for explanation of the two demes, see F_{ST} and STRUCTURE analyses below). While 92.1% of dispersing newts moved less than 400 m, 6.9% moved more than 400 m and two individuals more than 1 km (i.e., 1.031 and 1.218 km). Curiously, newts recaptured in different ponds did not move to the nearest pond. The frequency histogram of observed maximum distances moved was better described by a power law (R^2 = .99) than by an exponential distribution (R^2 = .90), indicating higher proportions of short- and long-distance dispersers (Figure 3a).

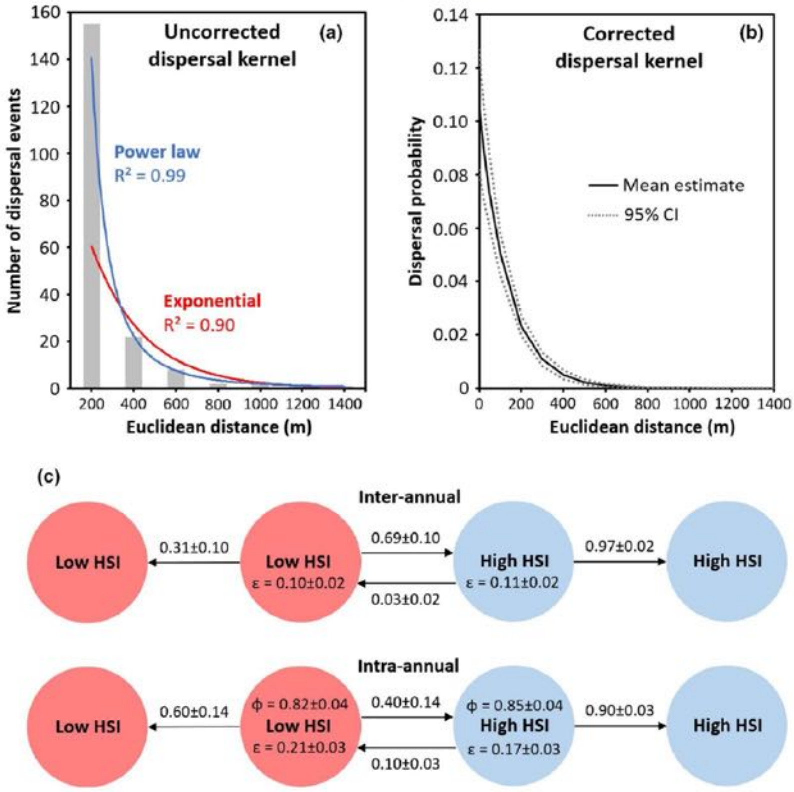


FIGURE 3 Dispersal kernels and context-dependent dispersal in a spatially structured population (SSP) of *Triturus cristatus* in Germany. (a) Uncorrected dispersal kernels fitted from raw capture–recapture data using power law and exponential functions. (b) Dispersal kernels corrected for detection issue estimated from a multistate capture–recapture model (mean and 95% CI are shown). (c) Context-dependent dispersal: effect of pond quality (HSI) on adult survival (φ), emigration (ε), and immigration (α) at inter- and intra-annual levels in the SSP. Immigration probability (α) is given along the arrow that represents the direction of dispersal movements. We provide model-averaged demographic parameters (mean and *SE*) from the multi-event models presented in Table 2. Circles correspond to low-HSI ponds (in orange; on the left) and high-HSI ponds (in blue; on the right)

3.1.2 | Estimating dispersal distances

The multistate model {Φ (.), p (Pond), Ψ (Dist)} indicating pond-specific recapture probabilities and distance-dependent dispersal probabilities was best supported by the data (w = 0.8080; Table 1). Weekly survival probability was constant at 0.995 (95% CI 0.993–0.996). Consequently, annual survival was extrapolated to 0.771 (95% CI 0.770–0.773). Detection probabilities varied among ponds, ranging from 0.004 to 0.210 (though the detection probability of one pond could not be estimated because of a lack of recaptures). Dispersal probability decreased with increasing distance between ponds ($\text{logit}(\Psi) = -2.1509334 - 0.0078935 \times \text{Distance}$; Figure 3b).

3.1.3 | Estimating the proportion of dispersing individuals

Multi-event models (all parameters in Table S3) indicated that the proportion of individuals with a dispersing phenotype (i.e., those that have dispersed at least once during their lifetime) was 0.35 (95% CI 0.22–0.50), while the proportion of fully site-faithful individuals (i.e., the nondispersing phenotype) was 0.65 (95% CI 0.49–0.78). The probability that an individual with a dispersing phenotype changed pond was 0.32 (95% CI 0.19–0.49) and 0.68 (95% CI 0.36–0.89) at the intra- and inter-annual level, respectively.

3.1.4 | Evaluating the effect of habitat quality on survival, emigration and immigration

The best-supported multi-event model was {φ (.), ε (.), α (HSI), p (Y)} (Table 2). As its Akaike weight was 0.30, the demographic parameters were model-averaged. Our results indicate that survival probability was similar in low-HSI (0.82 ± 0.04) and high-HSI (0.85 ± 0.04) ponds. Emigration probability was higher in low-HSI (0.21 ± 0.03) than in high-HSI (0.17 ± 0.03) ponds at the inter-annual level; by contrast, emigration probability was similar in low-HSI (0.10 ± 0.02) and high-HSI (0.11 ± 0.02) ponds at the intra-annual level. Furthermore, immigration probability was strongly dependent on HSI (Figure 3c). At the inter-annual level, individuals from both low-HSI and high-HSI ponds preferentially immigrated into high-HSI ponds rather than into low-HSI ponds. At the intra-annual level, individuals from high-HSI ponds more frequently immigrated into high-HSI ponds rather than into low-HSI ponds. By contrast, the probability of immigrating into the two types of ponds was more balanced in individuals that emigrated from low-HSI ponds (Figure 3c).

3.1.5 | Evaluating the effect of habitat quality on occurrence of reproduction

We first selected a model that best explained the detection process, while keeping occupancy and reproduction probabilities constant.

Akaike weights (w) suggested that model {ψ (.), R (.), δ (Y*cs), p^1 (cs), p^2 (cs)} was best supported by the data (w = 0.99; Table S4). This model suggests that the probabilities of detecting newts in ponds occupied with reproduction, as well as in occupied ponds without reproduction, depended on capture session (2nd vs. 3rd *cs*). However, the probability of correctly identifying ponds as reproduction sites varied among *cs* and years. We used the top-ranking detection model to determine the effects of connectivity (S), HSI and pond surface area (Area) on occupancy and reproduction probabilities. The model that best explained the data (w = 0.98; Table 3) showed that the probabilities of pond occupancy and reproduction increased with increasing habitat quality (Figure 4). In contrast, models assuming that occupancy or reproduction probabilities depend on connectivity or patch size received little support ($w \leq 0.02$; Table 3).

3.2 | Genetic analyses within the SSP

3.2.1 | Genetic diversity estimates

The microsatellite loci analysed for the ponds within the SSP did not significantly deviate from HWE except for locus Tcri46 in pond NE_12 (p = .001, homozygote excess). However, the analysis with MICROCHECKER found homozygote excess on this locus in several localities (ponds NE_4, NE_7, NE_11, NE_14, NE_20), and also for Tcri27 (ponds NE_4, NE_19, NE_20), which was probably caused by high dispersal rates among the ponds of the SSP. Three loci were monomorphic in certain localities: Tcri13 in pond NE_17; Tc58 in ponds NE_7 and NE_15; and Tc85 in ponds NE_1, NE_4, NE_15 and NE_17 (Table S5). As this pattern was not consistent across ponds, the occasionally monomorphic loci were kept for subsequent analyses. Loci Tc50 and Tcri36 were in linkage disequilibrium in 13 of 24 ponds within the SSP, as were loci Tc58 and Tc68b in seven ponds, indicating that alleles on these loci were nonrandomly associated (Table S6).

Genetic diversity was relatively constant between all ponds within the SSP, with pond NE_3 exhibiting the lowest and pond NE_17 the highest diversity (A_r 1.95–2.4, mean 2.41; H_E 0.45–0.65, mean 0.65; Table 4).

3.2.2 | Population genetic structure analyses

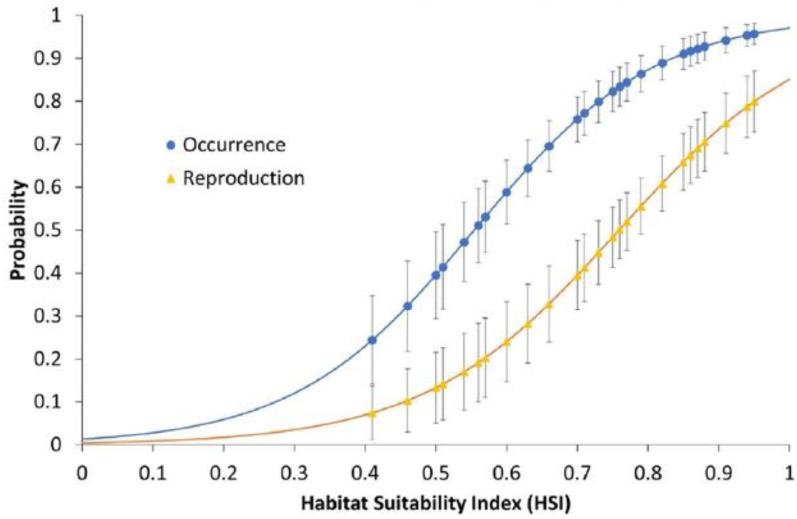
Pairwise F_{ST} values between ponds ranged from 0 to 0.018 and were not always significant, indicating relatively weak population structure within an area of 7.7 km^2 covered by the SSP (Figure 5a). STRUCTURE analysis indicated the existence of two genetic clusters within the SSP (Figures S1 and S2). One genetic cluster was located in the southwestern part of the nature reserves (SW deme; within the *NSG Stellmoorer Tunneltal*) and the other was in the northeastern

TABLE 3 Selection of multiseason multistate models for estimating occupancy and breeding probabilities of *Triturus cristatus* in different ponds within the spatially structured population

Model	ΔAIC	w	k
ψ (HSI), R (HSI), δ (Y*cs), p^1 (cs), p^2 (cs)	0.00	0.9810	14
ψ (HSI), R (Area), δ (Y*cs), p^1 (cs), p^2 (cs)	8.97	0.0111	14
ψ (HSI), R (.), δ (Y*cs), p^1 (cs), p^2 (cs)	10.28	0.0057	13
ψ (HSI), R (S), δ (Y*cs), p^1 (cs), p^2 (cs)	12.28	0.0021	14
ψ (.), R (HSI), δ (Y*cs), p^1 (cs), p^2 (cs)	20.14	0	13
ψ (Area), R (HSI), δ (Y*cs), p^1 (cs), p^2 (cs)	21.75	0	14
ψ (S), R (HSI), δ (Y*cs), p^1 (cs), p^2 (cs)	22.00	0	14
ψ (.), R (Area), δ (Y*cs), p^1 (cs), p^2 (cs)	29.31	0	13
ψ (.), R (.), δ (Y*cs), p^1 (cs), p^2 (cs)	30.67	0	12
ψ (Area), R (Area), δ (Y*cs), p^1 (cs), p^2 (cs)	30.92	0	14
ψ (S), R (Area), δ (Y*cs), p^1 (cs), p^2 (cs)	31.18	0	14
ψ (Area), R (.), δ (Y*cs), p^1 (cs), p^2 (cs)	32.27	0	13
ψ (S), R (.), δ (Y*cs), p^1 (cs), p^2 (cs)	32.54	0	13
ψ (.), R (S), δ (Y*cs), p^1 (cs), p^2 (cs)	32.67	0	13
ψ (Area), R (S), δ (Y*cs), p^1 (cs), p^2 (cs)	34.27	0	14
ψ (S), R (S), δ (Y*cs), p^1 (cs), p^2 (cs)	34.54	0	14

AIC of the best model was 565.53. Occupancy probability (ψ) and reproduction probability (R) were modelled either as constant (.) or as a function of habitat suitability (HSI), pond surface area (Area) or connectivity (S), while using the structure of the best detection model {ψ (.), R (.), δ (y*cs), p^1 (cs), p^2 (cs)}, where the probability of detecting newts in ponds occupied without reproduction (p^1), as well as in ponds with successful reproduction (p^2) depended on *cs* and the probability of correctly identifying ponds as breeding sites varied among Y and *cs*. HSI: habitat suitability index; Area: pond surface area; S: connectivity; Y: year; *cs*: capture session. AIC: Akaike's information criterion; ΔAIC: difference of the AIC value of the model with the lowest AIC score and the given model; *w*: Akaike weight; *k*: number of model parameters.

FIGURE 4 The relationship between pond quality (HSI) and occurrence and reproduction probabilities of *Triturus cristatus*. Symbols represent mean estimates and *SE*. Occurrence and reproduction probabilities were estimated for HSI values observed at 33 ponds within the spatially structured population over 3 years of monitoring



part (NE deme; mainly within the *NSG Höltigbaum*; see Figure 2). While the occupied ponds in the SW deme all lie within a radius of 300 m and are between 32 and 135 m from the nearest used pond, the ponds in the NE deme spread over almost 3 km and are between 48 and 759 m from the next used pond. The analysis from CLUMPP revealed a high similarity among the 10 replicate runs for $k = 2$ ($H' = 0.964$).

3.2.3 | Spatial extent of effective dispersal and Mantel autocorrelogram

The autocorrelogram based on PhiST indicated a spatial pattern of genetic isolation by distance, with significant positive spatial autocorrelation occurring up to 2 km (Figure 5c). This result suggests that, within the SSP, the spatial extent of effective dispersal is less than 2 km, which is congruent with the maximum noneffective dispersal distance recorded by our mark–recapture data (about 1.2 km).

3.2.4 | Relatedness structure and IBD analyses

Relatedness analyses revealed that the mean relatedness coefficient was close to 0 within each pond (Figure S3). The linear mixed model indicated that mean relatedness was higher within (coefficient: 0.007 ± 0.0008) than between ponds (LR test: $df = 1$, $\chi^2 = 124.25$, $p < 2.2e{-}16$). However, the proportion of variance explained by the factor WBP ("within vs. between pond") was very low (marginal $R^2 = .0003$). Furthermore, IBD analyses based on the individual pairwise relatedness coefficient showed that the relatedness level decreased with Euclidean distance (coefficient slope: −0.003 ± 0.0002; LR test: $df = 1$, $\chi^2 = 124.25$, $p < 2.2e{-}16$), but again the proportion of variance explained by the Euclidean distance was negligible (marginal $R^2 = .0005$). Overall, our analyses revealed a weak but still significant relatedness structure and IBD pattern.

3.2.5 | Effective dispersal rates between genetic clusters and first-generation migrants

We calculated effective dispersal rates between the NE and the SW deme. Using BIMR, the run with the lowest Bayesian deviance (D_{assign}) indicated no asymmetric movement between the two demes (95% HPDIs were overlapping): the mean effective dispersal rate was 0.250 (±0.029) from the NE to the SW deme and 0.394 (±0.022) from the SW to the NE deme. By contrast, BAYESASS indicated asymmetric effective dispersal rates: the mean dispersal rate was 0.286 (±0.007) from the NE to the SW deme while it was 0.045 (±0.004) from the SW to the NE deme. No F_0 migrants were detected between the two demes.

3.3 | Genetic analyses at the regional scale

3.3.1 | Genetic diversity estimates

The studied ponds were overall in accordance with HWE except for locus Tcri46 (site 3, homozygote excess, $p < .002$) and locus Tc70 (site 4, heterozygote excess, $p < .002$). The analysis with MICROCHECKER additionally showed a homozygote excess for locus Tcri36 at sites 6 and 7. Although these loci did not significantly deviate from HWE, it suggests the presence of null alleles. Locus Tc66 was monomorphic in the sampled individuals from site 7 and locus Tc85 was monomorphic for sites 3 and 7 (Table S5). The data indicated significant linkage: between Tc50 and Tcri36 in six ponds, between Tc58 and Tc68b in five ponds, and between Tcri46 and Tcri35 in four ponds (Table S6). Linkage disequilibrium was also found between other loci, but this was less consistent across ponds.

Genetic diversity varied between sampling sites, with the highest diversity observed each at sites 1, 4 and 5 ($A_r = 6.4$, $H_E = 0.6$), and the lowest observed at site 7 ($A_r = 3.3$, $H_E = 0.4$; Table 4). No significant inbreeding was detected.

TABLE 4 Genetic diversity estimates of the seven regional sampling sites and 19 ponds within the spatially structured population (with N > 10 sampled individuals)

Sites	N	A_r	P_A	H_O	H_E	F_{IS}	F_{IS} 95% CI−	F_{IS} 95% CI+
Regional level								
1	50	6.404	5	0.633	0.635	0.005	−0.048	0.04
2	24	5.638	4	0.603	0.594	−0.012	−0.084	0.017
3	54	5.175	4	0.601	0.593	−0.012	−0.065	0.022
4	57	6.454	4	0.664	0.638	−0.049	−0.093	−0.022
5	65	6.447	3	0.627	0.611	−0.026	−0.071	0.004
6	52	4.941	7	0.578	0.575	−0.015	−0.067	0.022
7	39	3.31	4	0.452	0.455	−0.001	−0.074	0.055
Within the SSP								
NE_1	10	2.372	NA	0.612	0.576	−0.066	−0.22	−0.04
NE_4	98	2.496	1	0.642	0.64	−0.008	−0.05	0.023
NE_6	33	2.497	5	0.648	0.649	0.007	−0.07	0.049
NE_7	30	2.48	NA	0.619	0.627	0.012	−0.06	0.049
NE_10	36	2.547	NA	0.684	0.653	−0.056	−0.11	−0.03
NE_11	39	2.469	NA	0.618	0.626	0.011	−0.04	0.036
NE_12	10	2.448	NA	0.659	0.611	−0.05	−0.23	−0.02
NE_17	33	2.565	NA	0.663	0.65	−0.02	−0.09	0.019
NE_18	13	2.47	NA	0.647	0.612	−0.042	−0.18	−0.01
NE_19	39	2.473	NA	0.634	0.625	−0.02	−0.08	0.015
NE_20	188	2.491	4	0.623	0.635	0.023	0	0.045
NE_21	37	2.514	NA	0.657	0.636	−0.034	−0.09	−0.01
NE_22	25	2.423	NA	0.604	0.604	0.007	−0.08	0.056
SW_4	24	2.427	NA	0.596	0.608	0.033	−0.04	0.072
SW_5	25	2.47	NA	0.614	0.626	0.031	−0.06	0.086
SW_6	71	2.47	NA	0.613	0.628	0.03	−0.01	0.059
SW_7	33	2.475	1	0.654	0.632	−0.033	−0.09	0.005
SW_8	46	2.395	1	0.615	0.61	−0.011	−0.07	0.024
SW_9	18	2.379	NA	0.62	0.589	−0.041	−0.13	−0.01

Allelic richness A_r, private alleles P_A, observed and expected heterozygosity (H_O, H_E), inbreeding coefficient (F_{IS}) with confidence intervals (95%). Ponds were named according to the deme they were assigned to (NE, northeastern deme; SW, southwestern deme).

3.3.2 | Population genetic structure analyses

F_{ST} values ranged between sites from 0.1 to 0.17 and were all significant, indicating a relatively strong population structure within this area of 350 km^2 (Figure 5b). STRUCTURE analysis of all seven sites indicated three distinct genetic clusters at the highest level of genetic structuring (Figures S4 and S5). While sites 6 and 7 represent distinct clusters each, sites 1–5 formed a single cluster, hereafter called cluster 1 (see Figure 1). While CLUMPP analysis revealed a high similarity of clustering solutions across the 10 replicate runs for $k = 3$ ($H' = 0.996$), the mean likelihood L(K) value was highest for $k = 5$ (Figure S5). The structure analysis indicated the presence of three distinct subclusters within cluster 1: subcluster 1.1 (sites 1 and 2), subcluster 1.2 (site 3) and subcluster 1.3 (sites 4 and 5; see Figure 1).

3.3.3 | Spatial extent of effective dispersal and Mantel autocorrelogram

The autocorrelogram based on PhiST indicated a spatial pattern of genetic isolation by distance, with significant positive spatial autocorrelation occurring up to 5 km (Figure 5d). This pattern indicates that, at the regional level, the spatial extent of effective dispersal is less than 5 km.

3.3.4 | Effective dispersal rates between genetic clusters and first-generation migrants

Our results showed that effective dispersal rates among the seven sites were very low. Using BIMR, the run with the lowest Bayesian deviance

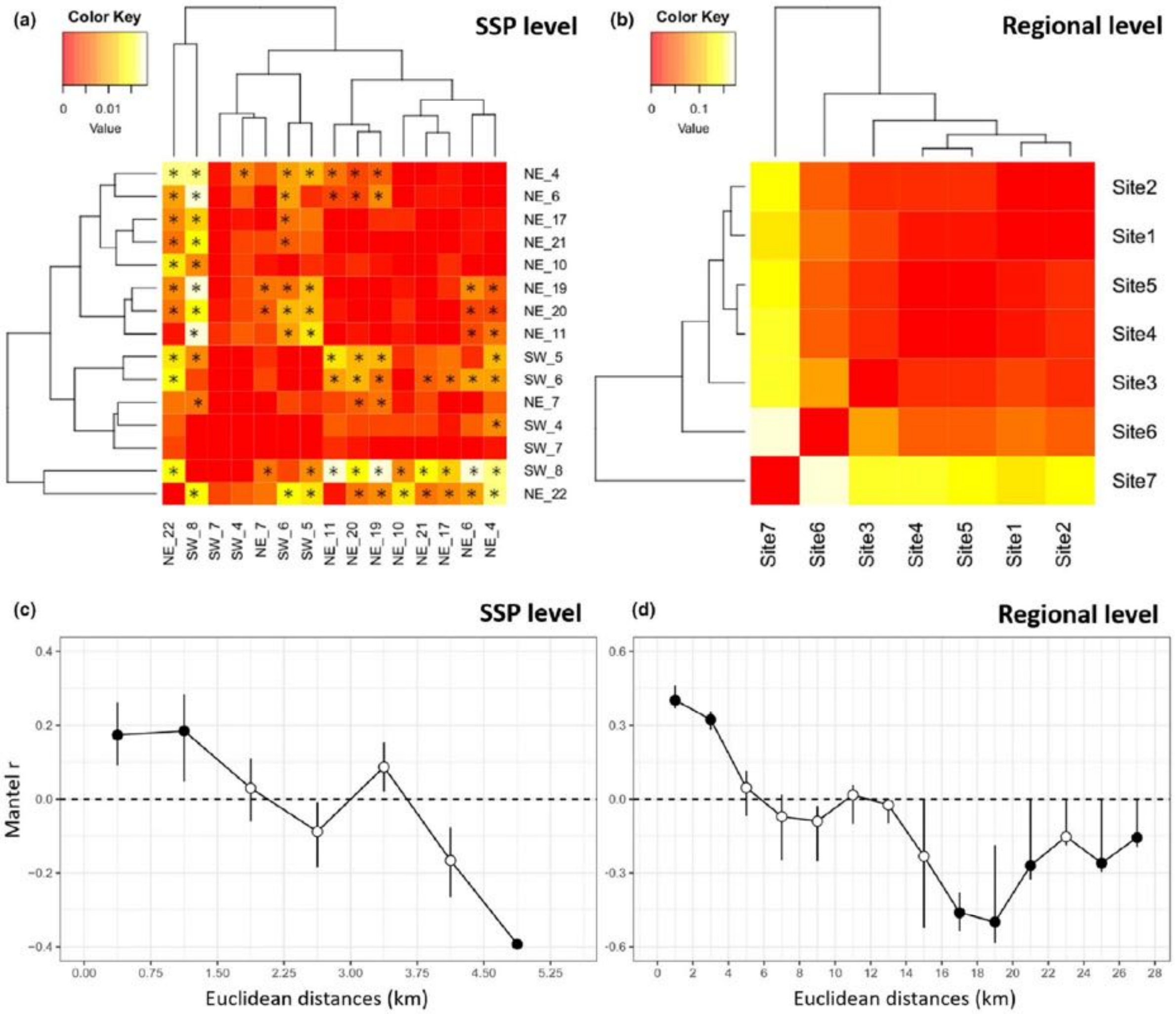


FIGURE 5 Genetic structure at both SSP and regional levels. (a, b) Heatmap and dendrogram of the pairwise F_{ST} distances. (a) Between 15 ponds at the level of the spatially structured population (only populations with $N \geq 20$ individuals were included); ponds were named according to the deme they were assigned to (NE: northeastern deme; SW: southwestern deme); asterisks indicate statistical significance ($p \leq .05$). (b) Between seven sites on the regional level (all values were significant). (c, d) Mantel autocorrelograms showing genetic autocorrelation according to Euclidean distance between ponds (c) and sites (d). The full and empty points show the Euclidean distances where genetic autocorrelation is significant and nonsignificant, respectively

(D_{assign}) indicated low effective dispersal rates (Figure 6a), ranging from 0.002 (±0.003, from cluster 3 to cluster 1) to 0.021 (±0.014, from cluster 1 to cluster 3). Similarly, BAYESASS indicated very low effective dispersal rates (Figure 6b), ranging from 0.005 (±0.004, from cluster 1 to 2) to 0.023 (±0.011, from cluster 2 to 3).

Furthermore, we found that effective dispersal rates among the three genetic subclusters within cluster 1 were also generally low. Program BIMR indicated low effective dispersal rates (Figure 6a), ranging from 0.002 (±0.005, from subcluster 1.3 to subcluster 1.2) to 0.309 (±0.054, from subcluster 1.1 to subcluster 1.3). Similarly, BAYESASS indicated very low effective dispersal rates (Figure 6b), ranging from 0.009 (±0.009, from subcluster 1.2 to 1.1) to 0.031 (±0.018, from subcluster 1.3 to 1.1).

The analysis of F_0 migrants using the software GENECLASS 2.0 identified two F_0 migrants among clusters. One individual probably dispersed from cluster 1 to cluster 2, which is a distance of around 5 km. The second seems to have dispersed at least 16 km from cluster 1 to cluster 3. No F_0 migrants were detected among the three subclusters within cluster 1.

4 | DISCUSSION

The type of SSP is mainly determined by the dispersal of individuals. Here, we used the analysis of dispersal as a key to characterize the type of SSP of a pond-breeding amphibian, the great crested newt.

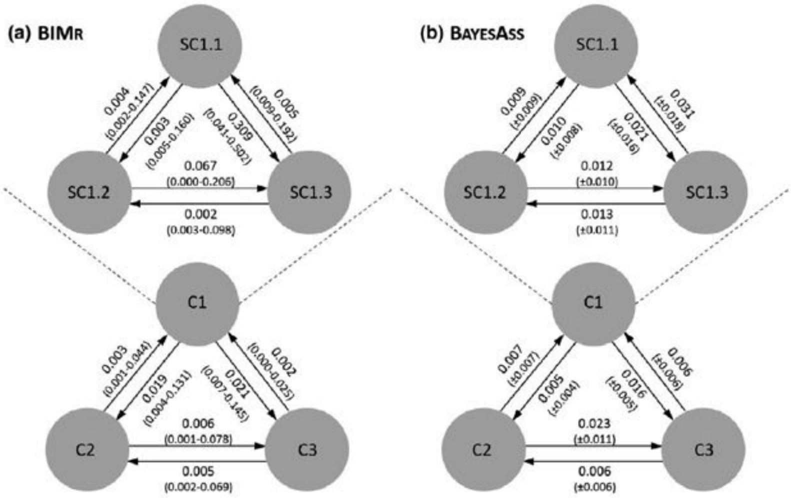


FIGURE 6 Effective dispersal rates at the regional level. We used BIMR and BAYESASS to estimate effective dispersal among the three genetic clusters (C1, C2 and C3) and the three genetic subclusters (SC1.1, SC1.2 and SC1.3) within cluster 1 (C1). Mean and highest posterior density interval are given for BIMR and mean *SE* are provided for BAYESASS

Within the SSP, we found that dispersal rates were both relatively high and context-dependent. If newts dispersed, individuals preferentially immigrated into high-quality ponds, a move likely to increase their own fitness. Although a few rare events of long-distance dispersal (>1 km) were detected, dispersal mostly comprised short-distance movements of up to 400 m. Overall, these dispersal patterns indicate that the SSP behaves like a patchy population where subpopulations at each pond are demographically interdependent. This demographic system led to a weak genetic structure and low relatedness of individuals within the SSP, although an IBD signal was nevertheless detected. By contrast, at the regional level our analyses revealed a strong hierarchical genetic structure with limited admixture and very few first-generation (F_0) migrants. In addition, effective dispersal rates were also rather low, even between spatially close sites (within 3–6 km), suggesting the presence of several independent demographic units.

4.1 | Context-dependent dispersal as a behaviour to increase reproductive success

Our analyses revealed that in the SSP studied, dispersal was context-dependent (i.e., "informed dispersal" *sensu* Clobert et al., 2009) and depended on HSI, the index of habitat quality. Although habitat quality marginally affected emigration probability, it strongly influenced immigration probability. Individuals preferentially immigrated into high-quality ponds where abundance is generally higher and body condition lower than in low-quality ponds (Unglaub et al., 2018). Overall, our results suggest that adult pond choice does not result from a strategy to maximize their own survival. Annual survival probability was both high and independent of pond habitat quality. It was 0.82 and 0.85 in low- and high-quality ponds respectively, which is similar to survival values estimated in the most long-lived populations of *Triturus cristatus* (Cayuela, Besnard, et al., 2020: 0.83 and 0.87 in populations from southern England and western France respectively). By contrast, our analyses indicate that context-dependent dispersal is associated with reproductive success in ponds: individuals more frequently immigrate in ponds with a high HSI where the reproduction probability is highest. This result is consistent with previous studies that showed amphibians actively select breeding waterbodies with biotic and abiotic characteristics that increase offspring fitness at premetamorphic stages (Buxton & Sperry, 2017). For example, in the yellow-bellied toad (*Bombina variegata*), adult emigration and immigration probabilities are determined by pond hydroperiod (Tournier et al., 2017) and anthropogenic disturbance (Boualit et al., 2019); both these factors have a strong effect on breeding probability and toadlet production.

Although the proximal mechanisms involved in pond selection during the immigration phase have not been fully deciphered, studies suggest that *T. cristatus* adults could use multiple cues to assess pond quality for reproduction. In particular, individuals could use conspecific and heterospecific density as a "public information" (*sensu* Valone, 1989) to adjust their emigration and immigration decisions (Cayuela, Grolet, et al., 2018; Cayuela, Schmidt, et al., 2019). Moreover, pond odour could also be used to assess pond quality during the immigration phase, since amphibians in general are able to assess the chemical signature of their natal pond (Sinsch, 1991, 2006) as well as the odour of predators (Buxton & Sperry, 2017).

Overall, our study and previous work (Barrile et al., 2021; Boualit et al., 2019; Tournier et al., 2017) suggest that amphibians adjust their dispersal decisions according to environmental and/or social cues reflecting local fitness prospects in the aquatic patches used for reproduction (Cayuela, Valenzuela-Sánchez, et al., 2020). Those results are congruent with the conclusions drawn by a growing number of studies on vertebrates and invertebrates that show dispersal to be a plastic phenotypic trait (Saastamoinen et al., 2018) allowing organisms to respond to the spatiotemporal heterogeneity of their habitat in fragmented landscapes (Baguette et al., 2013; Cote et al., 2017; Hendrix et al., 2017).

4.2 | Demographic consequences of context-dependent dispersal

Our analyses showed that 35% of the individuals dispersed at least once during the 3-year study. Annual survival in the studied SSP is estimated to be 0.77. This means that 77% of the individuals survive 1 year, 59% 2 years and 45% 3 years. Thus, the study period covered half of the lifespan of newts in this SSP. This proportion of dispersing individuals is half that estimated by Denoël et al. (2018; 0.70) using the same modelling approach for a *T. cristatus* SSP in Belgium. In contrast, it is much higher than the proportion of dispersers observed in another SSP in western Germany (Unglaub et al., 2015; 11 dispersing individuals out of 1838 individuals marked). Furthermore, the dispersal kernel estimated in our study shows that most dispersal movements are shorter than 200 m, although rare long-distance dispersal events (>1.2 km) were also detected. These results are congruent with those of Cayuela, Besnard, et al. (2020), indicating that dispersal movements mostly occurred among spatially close ponds (distance between ponds <100 m). Taken together, the studies of Denoël et al. (2018), Cayuela, Besnard, et al. (2020) and the present study suggest that *T. cristatus* SSPs tend to behave as patchy populations when geographical distance between ponds is short (<200 m). In this situation, subpopulations of breeders occupying the different ponds of a network are thus interdependent demographic units connected by high migrant flows (Harrison, 1991).

Our results also showed that despite the asymmetric dispersal rate among ponds, the dispersal pattern in the SSP did not meet the theoretical expectations of the source–sink model even though successful reproduction (i.e., presence of larvae) was observed only in high-quality ponds (Kawecki, 2004; Pulliam, 1988). Instead of mainly immigrating into low-quality ponds, most dispersing individuals from high-quality ponds preferentially immigrated in ponds of similar quality (90% and 97% at the intra- and inter-annual level, respectively). By choosing high-quality ponds, individuals may subsequently maximize their reproductive success. It is nevertheless possible that subsequent marginal disperser inflow from high-quality ponds (10% and 3% at the intra- and inter-annual level respectively) contributes to the long-term persistence of subpopulations occupying low-quality ponds (where there is often no successful reproduction). Further demographic modelling should be performed to evaluate whether this small proportion of immigrants allows effective compensatory immigration, that is an immigrant inflow sufficient to compensate depauperate natality and maintain stable population growth rate ($\lambda \geq 1$) in subpopulations experiencing suboptimal environmental conditions (Kawecki, 2004; Runge et al., 2006).

Overall, our results showed that the studied SSP behaves as a patchy population rather than a Levins-type metapopulation, which supports the idea that SSPs which meet the Levins-type metapopulation assumptions are rare in the wild (Fronhofer et al., 2012), particularly in amphibians (Smith & Green, 2005). Our analyses also revealed that the studied SSP does not present the typical pattern of asymmetric dispersal expected under Pulliam's (1988) source–sink model. However, it is possible that the low dispersal rates observed between high- and low-quality ponds is sufficient to allow the persistence of populations in low-quality ponds.

4.3 | Genetic consequences of high context-dependent dispersal within the SSP

Our analyses show that high levels of context-dependent dispersal are associated with a weak genetic structure in the patchy population of *T. cristatus*. Although we detected two genetic clusters within the SSP, we found high levels of admixture and high effective dispersal rates between the two demes. In addition, our analyses reveal weak genetic relatedness in the SSP. Relatedness coefficients among individuals within ponds were close to 0, suggesting that subpopulations in ponds are mainly composed of unrelated adults. Furthermore, we show that the relatedness was slightly higher within ponds than between ponds, and that it slightly decreases with Euclidean distance between ponds. An IBD signal was also detected using a Mantel autocorrelogram based on PhiST, which showed that the spatial extent of effective dispersal was up to 2 km. Interestingly, this value was relatively close to the maximum distance of noneffective dispersal recorded using our capture–recapture data (1.2 km).

Together, these findings suggest that relatively high dispersal rates within the SSP lead to intense gene flow that weakens the genetic structure of the SSP and IBD patterns, and decreases the level of relatedness within ponds. This pattern is congruent with previous studies on amphibians showing that natal and reproductive dispersal modulates the strength of the genetic and relatedness structure within the SSP (Berven & Grudzien, 1990; Cayuela, Besnard, et al., 2020; Funk et al., 2005). However, the influence of dispersal on adaptative processes within amphibian SSPs is still poorly understood (Cayuela, Valenzuela-Sánchez, et al., 2020; Pabijan et al., 2020). Further genomic studies could help to investigate how dispersal intensity and context-dependency may erode (i.e., Tigano & Friesen, 2016) or favour (via "habitat matching choice"; Jacob et al., 2017) adaptation to breeding pond characteristics.

4.4 | Long-distance dispersal and genetic structure at the regional scale

At the regional level, we found a hierarchical genetic structure composed of three main clusters, of which one could be further subdivided into three subclusters. Admixture among the main clusters and among subclusters was rather limited and both BIMR and BAYESASS indicated low effective dispersal rates among them. Overall, these results indicate that clusters and subclusters behave like independent demographic/genetic units with limited gene flow between them. They are therefore consistent with previous studies that have highlighted strong genetic differentiation in *T. cristatus* at similar spatial scales (Haugen et al., 2020; Schön et al., 2011). In our study system, limited gene flow between demographic/genetic units separated from each other by relatively short Euclidean distances (from 3 to 27 km) is probably caused by the short distances that *T. cristatus* seem to move; dispersal kernels quantified at the SSP level showed that movements exceeding 1 km are rare events. Furthermore, physical barriers could also limit the movement of newts in the landscape matrix (Haugen et al., 2020), increasing genetic differentiation among clusters and subclusters.

4.5 | Implications for conservation

Identifying the major drivers sustaining the functioning of an SSP is crucial for conservation. Our results confirm previous findings that habitat quality has a strong impact on the demography, dispersal and genetic structure of amphibian populations (Cayuela, Besnard, et al., 2020). In keeping with earlier work (Unglaub et al., 2015, 2018), we find that in *T. cristatus*, higher habitat quality leads to greater abundance and higher reproductive success but is also correlated with a lower body condition of individuals. In contrast, individual survival does not appear to depend on habitat quality. Our finding that newts are more likely to both emigrate from low-quality patches and to immigrate into high-quality patches adds to earlier results which show they are more likely to emigrate from small populations than large populations (Cayuela, Schmidt, et al., 2019). Thus, to preserve *T. cristatus* populations in landscapes where habitat quality is poor, restoration of habitat quality is key to successful conservation. Habitat quality could be restored through the removal of predatory fish, removal of trees which shade the pond, or other actions that mitigate negative anthropogenic influences on habitat quality (Oldham et al., 2000). Enhancing habitat quality will increase the probability that a population produces larvae successfully and therefore recruitment. This will have positive effects on abundance and is likely to increase population viability (Halley et al., 1996; Karlsson et al., 2007). The restoration of habitat quality will also increase connectivity between sites due to increased dispersal rates. However, our study shows that most newts do not disperse farther than 400 m, and we found almost no dispersal between demes at the regional level. Therefore, conservation efforts should focus on sustaining dispersal between networks of ponds on a local scale rather than attempting to set up dispersal corridors between distantly located ponds. We suggest that conservation efforts should focus both on the restoration of habitat quality for existing populations and on the creation of new ponds, preferably on land with marginal value for biodiversity, close to existing ones to function as stepping stones and thus facilitate dispersal over longer distances (Rannap et al., 2009). This will lead to a functional network of populations and a viable patchy population (Griffiths & Williams, 2000; Halley et al., 1996; Karlsson et al., 2007).

5 | CONCLUSION

Our study provides one of the few empirical cases that illustrates the consequences of context-dependent dispersal on the demography, genetic structure and spatial patterns of relatedness of an SSP. Notably, our results show that a high context-dependent dispersal coupled with short-distance movement leads to the formation of a patchy population. At the regional level, this patchy population behaves like an independent demographic and genetic unit, having limited gene flow with neighbouring populations. Such population systems seem particularly common in amphibians (Smith & Green, 2005), and more generally in organisms with low vagility (e.g., reptiles and some insects, Bowne & Bowers, 2004) that occupy habitat patches in which distribution is spatially heterogeneous due to natural (e.g., variation in soil characteristics, temperature, and hygrometry) and anthropogenic causes (e.g., habitat alteration and habitat fragmentation). However, the long-term viability of many patchy populations is currently threatened by ongoing isolation and habitat loss resulting from anthropogenic changes in land use. Preserving habitat quality of local patches and facilitating dispersal and gene flow between local demographic units—even if limited—within patchy populations is of critical importance to facilitate demographic, genetic and evolutionary functioning, and to rescue these populations in the midst of anthropogenic stressors.

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AUTHOR CONTRIBUTIONS

S.S., B.R.S. and H.C. designed the study. B.U. performed field work. J.G. provided additional expertise and facilities. B.U., B.R.S. and H.C. analysed CMR-data, HSI data and performed demographic analysis. B.U., K.P., S.S. and H.C. analysed microsatellite loci data and performed population genetic analyses. B.U., B.R.S., S.S. and H.C. wrote the manuscript.

CONFLICTS OF INTERESTS

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Individual genotypes of microsatellite data, geographical coordinates of sampling locations of the SSP and at the regional level, capture–mark–recapture data and capture events data (presence/absence data), including HSI values of ponds within the SSP: https://datadryad.org/stash/share/aFMmXrRY9ew9IDAUZrPYbzfKq0cA_tCVJEsBCuleBNQ.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Supplemental Information for:

Context-dependent dispersal determines genetic and relatedness structure in an amphibian patchy population

Bianca Unglaub, Hugo Cayuela, Benedikt R. Schmidt, Kathleen Preißler, Julian Glos, Sebastian Steinfartz

Table of Contents:

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Extended methods

This section provides additional details on field and laboratory protocols as well as statistical analysis, complementing information in the main Methods section.

Study species and study sites

Study species

Triturus cristatus is a widely distributed European pond-breeding amphibian. The demographic parameters of this species are highly variable among populations: sexual maturity is reached at the age of two to four years and reproductive lifespan varies from 1 to 7 years (based on the survival estimates provided by Cayuela et al. 2020), with a maximum longevity of 16 years in the wild (Hagström, 1977). Skeletochronological studies found that the modal age of newts in natural populations was three years (e.g. Francillon-Vieillot, Arntzen, & Géraudie, 1990; Miaud, Joly, & Castanet, 1993). Males display a high dorsal crest as part of the species' sexual dimorphism and aggregate in leks during the time of reproduction (Hedlund, 1990). *Triturus cristatus* is listed in Annexes II and IV of the European Habitats Directive (92/43/EEC). Member states of the European Union are therefore required to monitor the conservation status of this species. In addition, *T. cristatus* is found on the Red Lists of many European countries (Arntzen *et al.,* 2009).

Study sites for demographic and genetic analyses

We analyzed dispersal and gene flow within a SSP occupying a set of 33 ponds located in two adjacent nature reserves *Höltigbaum* and *Stellmoorer Tunneltal* (Site 1), together covering an area of approximately 7.7 km². At the regional scale, we analyzed genetic structure of crested new populations by adding six additional sampling sites (Sites 2-7) distributed across Hamburg, Germany (Figure 1). The *Ahrensburger Tunneltal* (Site 2) follows to the north and belongs to the same geological unit, formed by meltwaters during the last ice age 15,000 years ago. The *Volksdorfer Teichwiesen* (Site 3) represents another tunnel valley formed by water from melting glaciers and is located about 3 km northwest from the SSP separated by human settlement. The two nature reserves *Wohldorfer Wald* (Site 4) and *Duvenstedter Brook* (Site 5) are situated in the north of Hamburg and belong to the same habitat network. Disconnected by the Alster valley, the nature reserve *Wittmoor* (Site 6) follows further to the west. It is located about 12 km northwest from the SSP. The conservation area *Die Reit* (Site 7) is situated roughly 16 km south of the SSP, separated by dense human settlement, freeways and the river Dove-Elbe. The coordinates of sampling sites are publicly available (see Data Accessibility section).

Demographic analyses within the SSP

Capture-recapture survey and data

Newts were captured using Ortmann's funnel traps (Drechsler, Bock, Ortmann, & Steinfartz, 2010) which were evenly distributed along the shoreline of a pond. The number of traps deployed per capture event varied according to pond perimeter (one trap per 10m shoreline), ranging from 1 to 27 traps. If a pond dried out during the sampling period, p was set to zero for this pond and

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cs. For individual recognition of newts during the CMR study, we used photographs of the ventral side of an individual which provides a natural marking in form of a highly variable but individually unique and stable color pattern through the time. Recaptured individuals were identified automatically by the software AMPHIDENT (Matthé *et al.*, 2017). The demographic data are publicly available (see Data Accessibility section).

Genetic analyses

DNA extraction and genotyping of microsatellite loci

Total genomic DNA was extracted using the sodium dodecyl sulfate (SDS)-proteinase K/ Phenol-Chloroform extraction method. Genomic DNA was stored in Tris-EDTA buffer (10 mM Tris-HCl, 0.1 mM EDTA, pH 8.0) and used for all subsequent reactions. Each individual sample was scored and analyzed for 17 microsatellite loci. Primers were combined in three multiplex mixes (Drechsler *et al.*, 2013). 10 µl Type-it Multiplex PCRs (Qiagen) containing 1 µl of genomic DNA were performed. The PCR profile was as follows: (1) 5 min at 95°C, (2) 30 s at 94°C, (3) 90 s at an annealing temperature of 60°C, (4) 60 s at 72°C, (5) return to step 2 for 30 times, (6) 30 min at 60°C. Obtained PCR products were diluted with 50-200 µl water depending on the strength of obtained PCR products. 1 µl of each diluted multiplex reaction was added to 20 µl of Genescan 500-LIZ size standard (Applied Biosystem) and then run on an ABI 3730 96-capillary or an ABI 3130 16-capillary automated DNA-sequencer. Allele scoring of microsatellite loci was performed using GENEMARKER software (SoftGenetics version 1.95). The genetic data are publicly available (see Data Accessibility section).

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Table S1: Number of genetic samples per sampling site for the (A) regional level; (B) SSP level.

(A)

Sampling site	Conservation area	N
Site 1	H/ST	50
Site 2	AT	25
Site 3	VT	55
Site 4	WW	64
Site 5	DB	66
Site 6	WM	54
Site 7	R	52
Σ	**7**	**366**

(B)

	Pond	N		Pond	N
NE deme	NE_1	11	**SW deme**	SW_2	5
	NE_3	3		SW_3	4
	NE_4	108		SW_4	29
	NE_6	40		SW_5	29
	NE_7	34		SW_6	85
	NE_10	40		SW_7	37
	NE_11	40		SW_8	50
	NE_12	10		SW_9	18
	NE_14	8		SW_11	1
	NE_15	6			
	NE_17	40			
	NE_18	14			
	NE_19	44			
	NE_20	208			
	NE_21	46			
	NE_22	40			
Σ	**16**	**692**		**9**	**258**

H/ST: Höltigbaum/Stellmoorer Tunneltal; AT: Ahrensburger Tunneltal; VT: Volksdorfer Teichwiesen; WW: Wohldorfer Wald; DB: Duvenstedter Brook; WM: Wittmoor; R: Die Reit.

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Table S2: Correlation between the five relatedness coefficients estimated from COANCESTRY.

	Wang	LynchLi	LynchRd	Ritland	QuellerGt
Wang	-	-	-	-	-
LynchLi	0.8186514	-	-	-	-
LynchRd	0.7069267	0.5963661	-	-	-
Ritland	0.4012647	0.4762232	0.7303109	-	-
QuellerGt	0.7026637	0.8897632	0.6222719	0.5379546	-

Table S3: Parameter estimates from the multi-event model developed by Denoël et al. (2018).

Parameter	Time	Estimate	95% CI		SE
r	-	0.6524	0.4954	0.7820	0.0750
$1-r$	-	0.3476	0.2180	0.5046	0.0750
φ	Inter-annual	0.8454	0.7651	0.9018	0.0346
α	Intra-annual	0.6771	0.5047	0.8119	0.0805
$1-\alpha$	Intra-annual	0.3229	0.1881	0.4953	0.0805
α	Inter-annual	0.3191	0.1118	0.6356	0.1457
$1-\alpha$	Inter-annual	0.6809	0.3644	0.8882	0.1457
p	2012	0.1283	0.1140	0.1440	0.0076
p	2013	0.0910	0.0822	0.1008	0.0047
p	2014	0.0587	0.0509	0.0674	0.0042

r = proportion of fully site faithful individuals, $1-r$ = proportion of individuals with a dispersing phenotype (i.e., that have dispersed at least once during their lifetime), φ = survival probability, α = probability that an individual with a dispersing phenotype stayed pond between two capture sessions, $1-\alpha$ = probability that an individual with a dispersing phenotype changed of pond between two capture sessions, p = recapture probability. Estimate: Mean estimate; 95% CI: 95% Confidence Interval; SE: Standard error.

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Table S4: Selection of multiseason-multistate models for estimating detection parameters of *Triturus cristatus*.

Model	ΔAIC	*W*	*n*
ψ (.), R (.), δ (y*cs), p^1 (cs), p^2 (cs)	0.00	0.9893	12
ψ (.), R (.), δ (y*cs), p^1 (.), p^2 (.)	9.64	0.008	10
ψ (.), R (.), δ (cs), p^1 (cs), p^2 (cs)	12.72	0.0017	8
ψ (.), R (.), δ (y*cs), p^1 (y*cs), p^2 (y*cs)	14.4	0.0007	20
ψ (.), R (.), δ (y*cs), p^1 (y), p^2 (y)	16.52	0.0003	14

AIC of the best model was 596.2. Only models with $w > 0.01$ are shown. Occupancy probability (ψ) and reproduction probability (R) were held constant (.) to evaluate the effects of sampling time on detection parameters. Probability of correctly identifying a site as breeding site, given successful reproduction (δ) and the probabilities of detecting occupancy, given occupancy without reproduction (p^1) and with successful reproduction (p^2) were modelled as constant (.) or were allowed to vary between capture sessions (cs), years (y) or the interaction of both (y*cs). AIC: Akaike's information criterion; ΔAIC: difference of the AIC value of the model with the lowest AIC score and the given model; w: Akaike weight; n: number of parameters.

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Table S5. Exact test for deviations from Hardy-Weinberg-Equilibrium using a Markov chain. Microsatellite loci of *Triturus cristatus* from 7 regional sites and 25 ponds within the SSP are tested.

Locus	#Genot	H_o	H_e	p	SD	Steps done
			Regional level			
Site 1						
Tcri13	50	0.78	0.77313	0.98454	0.00038	100172
Tcri27	50	0.78	0.85455	0.55576	0.00123	100172
Tcri36	50	0.94	0.89354	0.90159	0.00058	100172
Tcri35	50	0.88	0.86283	0.62832	0.00131	100172
Tcri29	50	0.74	0.74182	0.2562	0.00109	100172
Tcri46	50	0.78	0.79232	0.43737	0.00084	100172
Tc68b	50	0.8	0.82586	0.47813	0.00143	100172
Tc66	50	0.68	0.63374	0.52402	0.0012	100172
Tc81	50	0.76	0.68889	0.95373	0.00065	100172
Tc52	50	0.64	0.58141	0.80551	0.00129	100172
Tc70	50	0.54	0.54929	1	0	100172
Tc50	50	0.9	0.94505	0.24766	0.0004	100172
Tc74	50	0.52	0.63919	0.44818	0.00111	100172
Tc85	50	0.1	0.09677	1	0	100172
Tc69	50	0.34	0.43616	0.03741	0.00058	100172
Tc58	50	0.28	0.27939	1	0	100172
Tc71	50	0.3	0.31091	1	0	100172
Site 2						
Tcri13	24	0.625	0.68528	0.15224	0.00073	100172
Tcri27	24	0.875	0.81294	0.20978	0.00066	100172
Tcri36	24	0.83333	0.86436	0.36794	0.00111	100172
Tcri35	24	0.79167	0.85018	0.82978	0.00099	100172
Tcri29	24	0.75	0.68262	0.70036	0.00128	100172
Tcri46	23	0.82609	0.79324	0.6467	0.00135	100172
Tc68b	24	0.79167	0.83954	0.23601	0.00129	100172
Tc66	24	0.625	0.56028	0.91651	0.00052	100172
Tc81	24	0.58333	0.60372	0.24054	0.00141	100172
Tc52	24	0.5	0.49468	0.82616	0.00137	100172
Tc70	24	0.625	0.52926	0.40999	0.00137	100172
Tc50	24	1	0.92465	0.94567	0.00019	100172
Tc74	24	0.375	0.55585	0.19568	0.00115	100172
Tc85	24	0.125	0.12145	1	0	100172

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Tc69	24	0.41667	0.33688	0.54019	0.0015	100172
Tc58	24	0.25	0.35106	0.01563	0.0003	100172
Tc71	23	0.26087	0.30048	0.51555	0.00162	100172
Site 3						
Tcri13	51	0.78431	0.73714	0.6734	0.00092	100172
Tcri27	52	0.80769	0.84149	0.11604	0.00087	100172
Tcri36	54	0.88889	0.85999	0.09679	0.00044	100172
Tcri35	53	0.79245	0.78814	0.52077	0.00151	100172
Tcri29	54	0.85185	0.70007	0.03525	0.00042	100172
Tcri46	54	0.62963	0.81395	**0.00026**	0.00005	100172
Tc68b	54	0.83333	0.75545	0.77356	0.0009	100172
Tc66	54	0.42593	0.43683	0.87323	0.00095	100172
Tc81	54	0.7037	0.66303	0.59626	0.00132	100172
Tc52	54	0.40741	0.392	0.20432	0.00118	100172
Tc70	54	0.53704	0.45466	0.23074	0.00121	100172
Tc50	54	0.87037	0.90689	0.36554	0.00082	100172
Tc74	54	0.53704	0.57321	0.59291	0.00162	100172
Tc85		This locus in monomorphic: not test done				
Tc69	54	0.27778	0.31914	0.32329	0.00156	100172
Tc58	54	0.44444	0.47439	0.7265	0.00146	100172
Tc71	54	0.42593	0.46452	0.35022	0.00145	100172
Site 4						
Tcri13	57	0.77193	0.68933	0.81228	0.00069	100172
Tcri27	57	0.77193	0.83683	0.60501	0.00098	100172
Tcri36	57	0.89474	0.88635	0.49558	0.00055	100172
Tcri35	57	0.82456	0.8744	0.5886	0.00121	100172
Tcri29	57	0.73684	0.73995	0.62808	0.00102	100172
Tcri46	52	0.88462	0.85119	0.41105	0.00102	100172
Tc68b	55	0.83636	0.82552	0.64033	0.00111	100172
Tc66	57	0.5614	0.57413	0.12458	0.00072	100172
Tc81	53	0.67925	0.63881	0.40217	0.00153	100172
Tc52	57	0.5614	0.47694	0.57944	0.00141	100172
Tc70	57	0.78947	0.51917	**0.00003**	0.00002	100172
Tc50	57	0.96491	0.94675	0.25061	0.0003	100172
Tc74	57	0.5614	0.59152	0.736	0.00085	100172
Tc85	57	0.2807	0.30787	0.01915	0.00038	100172
Tc69	57	0.38596	0.37587	0.728	0.00136	100172
Tc58	57	0.40351	0.35569	0.5849	0.00158	100172

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Tc71	57	0.38596	0.45412	0.48959	0.00139	100172
Site 5						
Tcri13	64	0.76562	0.7516	0.37744	0.00118	100172
Tcri27	64	0.85938	0.85482	0.22482	0.00074	100172
Tcri36	65	0.89231	0.88706	0.4583	0.00066	100172
Tcri35	64	0.90625	0.87131	0.5556	0.00099	100172
Tcri29	65	0.78462	0.77054	0.59222	0.00118	100172
Tcri46	61	0.77049	0.80084	0.43937	0.00108	100172
Tc68b	65	0.84615	0.8266	0.81543	0.00098	100172
Tc66	65	0.53846	0.53643	0.46436	0.00125	100172
Tc81	65	0.64615	0.58736	0.40999	0.00162	100172
Tc52	65	0.44615	0.39773	0.38551	0.00157	100172
Tc70	65	0.6	0.57102	0.72866	0.00136	100172
Tc50	65	0.89231	0.93679	0.05823	0.00021	100172
Tc74	65	0.70769	0.59845	0.52094	0.0011	100172
Tc85	65	0.15385	0.14657	1	0	100172
Tc69	65	0.23077	0.25009	0.26768	0.00115	100172
Tc58	65	0.23077	0.23769	0.36834	0.00132	100172
Tc71	65	0.38462	0.4384	0.35849	0.00172	100172
Site 6						
Tcri13	51	0.66667	0.63036	0.3727	0.00123	100172
Tcri27	51	0.84314	0.8212	0.83541	0.00093	100172
Tcri36	52	0.65385	0.76755	0.00332	0.00018	100172
Tcri35	52	0.73077	0.77857	0.17944	0.00092	100172
Tcri29	52	0.76923	0.74178	0.18018	0.0014	100172
Tcri46	50	0.66	0.70202	0.26216	0.00082	100172
Tc68b	52	0.71154	0.78715	0.74161	0.0009	100172
Tc66	52	0.53846	0.53491	0.82888	0.00124	100172
Tc81	52	0.61538	0.63088	0.04347	0.00072	100172
Tc52	52	0.40385	0.36277	0.86809	0.0009	100172
Tc70	52	0.44231	0.51363	0.61127	0.00151	100172
Tc50	52	0.90385	0.84354	0.67664	0.00096	100172
Tc74	52	0.61538	0.5913	0.45979	0.00099	100172
Tc85	52	0.42308	0.3876	0.83217	0.00126	100172
Tc69	52	0.34615	0.3329	0.75976	0.00152	100172
Tc58	52	0.01923	0.01923	1	0	100172
Tc71	52	0.48077	0.42252	0.50655	0.0015	100172
Site 7						

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Tcri13	38	0.76316	0.71123	0.9623	0.0006	100172
Tcri27	38	0.81579	0.77123	0.21544	0.00114	100172
Tcri36	39	0.5641	0.71362	0.01194	0.00022	100172
Tcri35	39	0.82051	0.72061	0.01314	0.00033	100172
Tcri29	39	0.64103	0.7003	0.03437	0.00062	100172
Tcri46	38	0.55263	0.65789	0.04866	0.00073	100172
Tc68b	38	0.57895	0.67965	0.43485	0.00149	100172
Tc66		This locus in monomorphic: not test done				
Tc81	39	0.4359	0.5045	0.474	0.00128	100172
Tc52	39	0.51282	0.47952	0.7445	0.00147	100172
Tc70	39	0.33333	0.3986	0.41265	0.00151	100172
Tc50	39	0.79487	0.7003	0.23978	0.00096	100172
Tc74	39	0.17949	0.1655	1	0	100172
Tc85		This locus in monomorphic: not test done				
Tc69	39	0.02564	0.02564	1	0	100172
Tc58	39	0.51282	0.4662	0.72901	0.00144	100172
Tc71	39	0.15385	0.14386	1	0	100172

SSP level

NE_1

Tcri13	10	0.9	0.78947	0.92644	0.00068	100172
Tcri27	10	0.9	0.80526	0.99434	0.00021	100172
Tcri36	10	0.8	0.85263	0.85116	0.00111	100172
Tcri35	10	0.9	0.88421	0.73136	0.00101	100172
Tcri29	10	0.6	0.66842	0.71575	0.00136	100172
Tcri46	10	0.6	0.76316	0.57921	0.002	100172
Tc68b	10	0.9	0.84737	0.69099	0.00125	100172
Tc66	10	0.6	0.56842	0.65161	0.00125	100172
Tc81	10	0.6	0.64737	1	0	100172
Tc52	10	0.3	0.54211	0.09639	0.00087	100172
Tc70	10	0.6	0.53158	1	0	100172
Tc50	10	1	0.96316	1	0	100172
Tc74	10	0.7	0.61053	1	0	100172
Tc85		This locus in monomorphic: not test done				
Tc69	10	0.6	0.46842	1	0	100172
Tc58	10	0.1	0.1	1	0	100172
Tc71	10	0.3	0.26842	1	0	100172

NE_3

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Tcri13		This locus in monomorphic: not test done				
Tcri27	2	0.5	0.5	1	0	100172
Tcri36	2	0.5	0.83333	0.33495	0.00137	100172
Tcri35	1	1	1	1	0	100172
Tcri29	2	0.5	0.83333	0.32618	0.00128	100172
Tcri46	2	1	1	1	0	100172
Tc68b	2	1	0.83333	1	0	100172
Tc66	2	0.5	0.5	1	0	100172
Tc81	2	0.5	0.5	1	0	100172
Tc52	2	1	0.83333	1	0	100172
Tc70	2	1	0.66667	1	0	100172
Tc50	2	1	1	1	0	100172
Tc74	2	0.5	0.5	1	0	100172
Tc85		This locus in monomorphic: not test done				
Tc69	2	1	0.66667	1	0	100172
Tc58	2	0.5	0.5	1	0	100172
Tc71	2	0.5	0.5	1	0	100172
NE_4						
Tcri13	98	0.76531	0.76515	0.26373	0.00114	100172
Tcri27	97	0.74227	0.83649	0.43283	0.00077	100172
Tcri36	97	0.8866	0.88986	0.36819	0.00077	100172
Tcri35	96	0.91667	0.87555	0.12565	0.00116	100172
Tcri29	96	0.75	0.75567	0.07387	0.00079	100172
Tcri46	96	0.70833	0.78343	0.02692	0.00035	100172
Tc68b	98	0.79592	0.82821	0.99209	0.0003	100172
Tc66	98	0.73469	0.66777	0.04535	0.0005	100172
Tc81	98	0.72449	0.69142	0.36755	0.00192	100172
Tc52	98	0.53061	0.50837	0.9654	0.00062	100172
Tc70	98	0.59184	0.54783	0.5495	0.00117	100172
Tc50	98	0.95918	0.94307	0.40915	0.00048	100172
Tc74	98	0.59184	0.57896	0.29622	0.00112	100172
Tc85	98	0.15306	0.14563	1	0	100172
Tc69	97	0.40206	0.47134	0.09459	0.00089	100172
Tc58	95	0.29474	0.30476	0.51936	0.00156	100172
Tc71	97	0.36082	0.33519	0.46066	0.00177	100172
NE_6						
Tcri13	33	0.78788	0.76224	0.33482	0.00127	100172
Tcri27	30	0.83333	0.84576	0.48518	0.00116	100172

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Tcri36	32	0.8125	0.91419	0.16652	0.00077	100172
Tcri35	32	0.90625	0.88542	0.51166	0.00185	100172
Tcri29	32	0.625	0.75843	0.0051*	0.00021	100172
Tcri46	31	0.77419	0.82232	0.01954	0.00029	100172
Tc68b	33	0.81818	0.83776	0.05998	0.00082	100172
Tc66	33	0.75758	0.69324	0.64918	0.00155	100172
Tc81	33	0.69697	0.68671	0.94842	0.00064	100172
Tc52	33	0.42424	0.53007	0.4091	0.00133	100172
Tc70	33	0.66667	0.54965	0.11351	0.00089	100172
Tc50	33	0.9697	0.95338	0.92766	0.00017	100172
Tc74	33	0.63636	0.61119	1	0	100172
Tc85	33	0.30303	0.29091	0.03744	0.00077	100172
Tc69	33	0.48485	0.46014	0.52624	0.00158	100172
Tc58	33	0.15152	0.29044	0.00739*	0.00023	100172
Tc71	33	0.36364	0.31469	1	0	100172
NE_7						
Tcri13	30	0.7	0.7548	0.7727	0.00102	100172
Tcri27	30	0.9	0.78079	0.81296	0.00098	100172
Tcri36	30	0.93333	0.91808	0.97638	0.00033	100172
Tcri35	29	0.93103	0.89413	0.776	0.00094	100172
Tcri29	29	0.7931	0.80641	0.18619	0.00067	100172
Tcri46	29	0.65517	0.8415	0.04584	0.00041	100172
Tc68b	30	0.76667	0.82203	0.24949	0.00139	100172
Tc66	30	0.73333	0.69605	0.77729	0.001	100172
Tc81	30	0.63333	0.6096	0.9022	0.00089	100172
Tc52	30	0.4	0.40791	0.83917	0.00113	100172
Tc70	30	0.46667	0.56893	0.47427	0.00172	100172
Tc50	30	1	0.94972	0.9326	0.00028	100172
Tc74	30	0.5	0.65367	0.2692	0.00161	100172
Tc85	30	0.16667	0.15989	1	0	100172
Tc69	30	0.36667	0.38644	0.82515	0.00115	100172
Tc58	29	0.2069	0.19177	1	0	100172
Tc71	30	0.36667	0.40621	0.26678	0.00147	100172
NE_10						
Tcri13	36	0.88889	0.79264	0.1271	0.00116	100172
Tcri27	36	0.88889	0.83646	0.58583	0.00096	100172
Tcri36	36	0.94444	0.88302	0.70879	0.00134	100172
Tcri35	36	0.94444	0.88967	0.19428	0.00146	100172

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Tcri29	36	0.88889	0.75626	0.25088	0.00117	100172
Tcri46	36	0.66667	0.76291	0.04095	0.0004	100172
Tc68b	36	0.77778	0.84155	0.57391	0.00091	100172
Tc66	36	0.61111	0.60837	0.23807	0.00108	100172
Tc81	36	0.61111	0.67801	0.04633	0.00061	100172
Tc52	36	0.5	0.48787	0.79037	0.00107	100172
Tc70	36	0.66667	0.53052	0.13884	0.00116	100172
Tc50	36	0.94444	0.95736	0.90449	0.00028	100172
Tc74	36	0.61111	0.64085	0.8349	0.00098	100172
Tc85	36	0.36111	0.33998	0.26517	0.00124	100172
Tc69	32	0.46875	0.47867	1	0	100172
Tc58	31	0.32258	0.27975	1	0	100172
Tc71	36	0.52778	0.48709	0.71116	0.00151	100172
NE_11						
Tcri13	39	0.82051	0.7952	0.67733	0.00121	100172
Tcri27	39	0.82051	0.83283	0.91909	0.00078	100172
Tcri36	39	0.94872	0.91275	0.56751	0.00091	100172
Tcri35	39	0.92308	0.88312	0.27649	0.0009	100172
Tcri29	39	0.61538	0.71062	0.18213	0.00108	100172
Tcri46	39	0.5641	0.73859	0.05265	0.00059	100172
Tc68b	39	0.84615	0.81285	0.34156	0.00126	100172
Tc66	39	0.76923	0.65468	0.32599	0.00137	100172
Tc81	39	0.61538	0.65534	0.32089	0.001	100172
Tc52	39	0.69231	0.54779	0.1196	0.00095	100172
Tc70	39	0.53846	0.56444	0.52955	0.00145	100172
Tc50	39	0.92308	0.95005	0.22055	0.00047	100172
Tc74	39	0.53846	0.671	0.16288	0.00076	100172
Tc85	39	0.17949	0.17083	1	0	100172
Tc69	39	0.23077	0.42857	0.00313*	0.0002	100172
Tc58	39	0.10256	0.09957	1	0	100172
Tc71	39	0.38462	0.35065	0.5239	0.00139	100172
NE_12						
Tcri13	10	0.9	0.78947	0.09561	0.00088	100172
Tcri27	10	1	0.85263	0.92585	0.0008	100172
Tcri36	10	1	0.91053	0.83761	0.00061	100172
Tcri35	10	1	0.84737	0.18338	0.00068	100172
Tcri29	10	0.8	0.8	0.45423	0.00106	100172
Tcri46	10	0.6	0.8	**0.00165**	0.00015	100172

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Tc68b	10	0.9	0.85789	0.90874	0.00078	100172
Tc66	10	0.6	0.63158	0.88183	0.00088	100172
Tc81	10	0.9	0.64737	0.03445	0.00062	100172
Tc52	10	0.6	0.48947	1	0	100172
Tc70	10	0.3	0.41579	0.48986	0.00119	100172
Tc50	10	0.8	0.92105	0.20712	0.0007	100172
Tc74	10	0.6	0.65263	0.83154	0.00119	100172
Tc85	10	0.1	0.1	1	0	100172
Tc69	10	0.1	0.26842	0.15885	0.00117	100172
Tc58	10	0.5	0.46842	0.30855	0.00133	100172
Tc71	10	0.5	0.47895	1	0	100172
NE_14						
Tcri13	8	1	0.76667	0.8774	0.00082	100172
Tcri27	8	0.75	0.75833	0.64228	0.00136	100172
Tcri36	8	0.625	0.84167	0.10595	0.00061	100172
Tcri35	8	1	0.86667	0.6701	0.0013	100172
Tcri29	8	0.75	0.68333	1	0	100172
Tcri46	8	0.375	0.775	0.02712	0.00048	100172
Tc68b	8	0.875	0.875	0.60509	0.00147	100172
Tc66	8	0.5	0.64167	0.68978	0.00128	100172
Tc81	8	0.625	0.7	0.80217	0.00134	100172
Tc52	8	0.625	0.51667	1	0	100172
Tc70	8	0.375	0.525	0.53029	0.00153	100172
Tc50	8	1	0.96667	0.05048	0.00021	100172
Tc74	8	0.5	0.575	0.66093	0.00146	100172
Tc85		This locus in monomorphic: not test done				
Tc69	8	0.625	0.49167	1	0	100172
Tc58		This locus in monomorphic: not test done				
Tc71	8	0.25	0.23333	1	0	100172
NE_15						
Tcri13	6	0.66667	0.77273	0.0196	0.00035	100172
Tcri27	6	1	0.83333	0.9454	0.00062	100172
Tcri36	6	1	0.87879	1	0	100172
Tcri35	6	0.66667	0.80303	0.75193	0.00146	100172
Tcri29	6	0.66667	0.75758	0.58196	0.00113	100172
Tcri46	6	0.83333	0.72727	1	0	100172
Tc68b	6	0.66667	0.80303	0.77251	0.00123	100172
Tc66	6	0.16667	0.16667	1	0	100172

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Tc81	6	0.66667	0.59091	0.64029	0.0015	100172
Tc52	6	0.33333	0.5303	0.51784	0.00133	100172
Tc70	6	0.83333	0.5303	0.39649	0.00145	100172
Tc50	6	0.83333	0.95455	0.35182	0.00083	100172
Tc74	6	0.66667	0.68182	0.6897	0.00144	100172
Tc85	6	0.33333	0.31818	1	0	100172
Tc69	6	0.66667	0.48485	1	0	100172
Tc58	6	0.16667	0.16667	1	0	100172
Tc71	6	0.5	0.68182	0.4952	0.00164	100172
NE_17						
Tcri13	33	0.81818	0.72261	0.66315	0.00111	100172
Tcri27	33	0.87879	0.81632	0.0918	0.00079	100172
Tcri36	33	0.9697	0.90769	0.3503	0.00057	100172
Tcri35	33	0.93939	0.87832	0.22741	0.00088	100172
Tcri29	33	0.81818	0.74592	0.80513	0.00129	100172
Tcri46	33	0.75758	0.81072	0.02018	0.00056	100172
Tc68b	33	0.72727	0.83916	0.03384	0.00048	100172
Tc66	33	0.75758	0.7021	0.22115	0.00103	100172
Tc81	33	0.69697	0.73473	0.07618	0.00064	100172
Tc52	33	0.54545	0.54965	0.54877	0.00167	100172
Tc70	33	0.51515	0.60699	0.27076	0.00093	100172
Tc50	33	0.9697	0.95245	0.51724	0.00031	100172
Tc74	33	0.63636	0.72354	0.02232	0.0005	100172
Tc85	33	0.12121	0.11795	1	0	100172
Tc69	33	0.42424	0.41772	1	0	100172
Tc58	33	0.30303	0.30723	1	0	100172
Tc71	33	0.39394	0.37855	1	0	100172
NE_18						
Tcri13	13	0.92308	0.79385	0.8168	0.0012	100172
Tcri27	13	0.92308	0.82769	0.84756	0.00087	100172
Tcri36	13	0.84615	0.93846	0.42892	0.0007	100172
Tcri35	13	0.92308	0.90769	0.95548	0.00058	100172
Tcri29	13	0.84615	0.82769	0.34113	0.00137	100172
Tcri46	13	0.69231	0.74769	0.88709	0.0008	100172
Tc68b	13	0.92308	0.86769	0.98842	0.00033	100172
Tc66	13	0.38462	0.48923	0.34619	0.00144	100172
Tc81	13	0.53846	0.49538	1	0	100172
Tc52	13	0.53846	0.53231	0.20836	0.00093	100172

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Tc70	13	0.46154	0.49231	1	0	100172
Tc50	13	1	0.97231	1	0	100172
Tc74	13	0.69231	0.63077	0.73129	0.00133	100172
Tc85	13	0.15385	0.15077	1	0	100172
Tc69	13	0.38462	0.42769	1	0	100172
Tc58	13	0.15385	0.27077	0.23492	0.00137	100172
Tc71	13	0.61538	0.44308	0.24124	0.00138	100172
NE_19						
Tcri13	39	0.71795	0.75957	0.20227	0.00158	100172
Tcri27	39	0.69231	0.82817	0.07573	0.00091	100172
Tcri36	39	0.92308	0.90942	0.09536	0.00026	100172
Tcri35	38	0.94737	0.88982	0.55922	0.00102	100172
Tcri29	39	0.74359	0.7619	0.74286	0.00085	100172
Tcri46	37	0.64865	0.74824	0.16724	0.00069	100172
Tc68b	39	0.89744	0.82085	0.48664	0.00144	100172
Tc66	39	0.64103	0.60273	0.81638	0.00082	100172
Tc81	39	0.5641	0.55145	0.27274	0.00117	100172
Tc52	39	0.64103	0.59207	0.39173	0.00099	100172
Tc70	39	0.53846	0.57542	0.92933	0.0008	100172
Tc50	38	0.97368	0.95825	0.6497	0.00019	100172
Tc74	39	0.69231	0.58974	0.47069	0.00087	100172
Tc85	39	0.12821	0.12288	1	0	100172
Tc69	39	0.41026	0.48651	0.30081	0.00131	100172
Tc58	39	0.35897	0.30636	0.6974	0.00157	100172
Tc71	39	0.25641	0.26374	1	0	100172
NE_20						
Tcri13	188	0.82979	0.77729	0.01965	0.00026	100172
Tcri27	188	0.74468	0.83329	0.15833	0.00067	100172
Tcri36	188	0.92021	0.89389	0.76276	0.00058	100172
Tcri35	187	0.8984	0.86939	0.03136	0.00064	100172
Tcri29	187	0.6738	0.73797	0.04024	0.00039	100172
Tcri46	187	0.6738	0.78449	0.02352	0.00035	100172
Tc68b	188	0.83511	0.83356	0.1321	0.00086	100172
Tc66	188	0.68085	0.67618	0.95019	0.00036	100172
Tc81	187	0.6631	0.65725	0.69212	0.0011	100172
Tc52	187	0.52941	0.52824	0.77204	0.00114	100172
Tc70	187	0.52941	0.56431	0.44865	0.00132	100172
Tc50	187	0.96791	0.94572	0.2596	0.00039	100172

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Tc74	185	0.54054	0.57763	0.50058	0.00079	100172
Tc85	188	0.16489	0.15956	0.75542	0.00118	100172
Tc69	188	0.44149	0.44501	0.40109	0.00096	100172
Tc58	187	0.22995	0.26407	0.00757*	0.00028	100172
Tc71	185	0.27027	0.28249	0.48771	0.00101	100172
NE_21						
Tcri13	37	0.86486	0.74676	0.03936	0.00041	100172
Tcri27	37	0.86486	0.80267	0.2032	0.00109	100172
Tcri36	37	0.89189	0.88634	0.76329	0.00048	100172
Tcri35	37	0.81081	0.85746	0.37168	0.0012	100172
Tcri29	37	0.75676	0.72307	0.46807	0.00124	100172
Tcri46	37	0.78378	0.79637	0.60936	0.00095	100172
Tc68b	37	0.91892	0.81673	0.96992	0.00043	100172
Tc66	37	0.62162	0.67864	0.26781	0.00107	100172
Tc81	37	0.64865	0.64754	0.13261	0.00071	100172
Tc52	37	0.51351	0.52684	0.5945	0.00125	100172
Tc70	37	0.43243	0.53277	0.52957	0.00165	100172
Tc50	37	0.97297	0.95631	0.97298	0.0002	100172
Tc74	37	0.64865	0.66642	0.83661	0.00115	100172
Tc85	37	0.16216	0.15439	1	0	100172
Tc69	37	0.64865	0.5846	0.34106	0.00157	100172
Tc58	37	0.27027	0.27545	1	0	100172
Tc71	37	0.35135	0.30211	0.70183	0.00151	100172
NE_22						
Tcri13	25	0.6	0.78367	0.0849	0.00088	100172
Tcri27	25	0.92	0.85633	0.73201	0.00107	100172
Tcri36	25	0.88	0.91918	0.96507	0.0005	100172
Tcri35	24	0.83333	0.75532	0.37913	0.00105	100172
Tcri29	25	0.84	0.72082	0.08929	0.00092	100172
Tcri46	25	0.8	0.80163	0.27436	0.00085	100172
Tc68b	25	0.96	0.82041	0.67956	0.00138	100172
Tc66	25	0.56	0.72735	0.01211	0.00035	100172
Tc81	25	0.36	0.54612	0.10074	0.00076	100172
Tc52	25	0.6	0.52816	0.17569	0.00108	100172
Tc70	25	0.64	0.63102	0.94296	0.00073	100172
Tc50	25	0.96	0.95184	0.53923	0.0005	100172
Tc74	25	0.56	0.60245	0.82472	0.00115	100172
Tc85	25	0.16	0.15429	1	0	100172

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Tc69	25	0.28	0.30776	0.57602	0.00169	100172
Tc58	This locus in monomorphic: not test done					
Tc71	25	0.32	0.3649	0.32236	0.00133	100172
SW_2						
Tcri13	5	0.8	0.71111	1	0	100172
Tcri27	5	1	0.88889	1	0	100172
Tcri36	5	1	0.93333	0.38	0.00081	100172
Tcri35	5	0.8	0.88889	0.61208	0.0012	100172
Tcri29	5	0.4	0.53333	0.31106	0.00125	100172
Tcri46	5	0.6	0.84444	0.36228	0.00196	100172
Tc68b	5	1	0.93333	1	0	100172
Tc66	5	0.6	0.64444	0.61106	0.00168	100172
Tc81	5	1	0.68889	0.43472	0.00163	100172
Tc52	5	0.4	0.37778	1	0	100172
Tc70	5	0.4	0.53333	1	0	100172
Tc50	5	1	0.86667	1	0	100172
Tc74	5	0.6	0.6	0.62133	0.00134	100172
Tc85	5	0.2	0.2	1	0	100172
Tc69	5	0.2	0.46667	0.33141	0.00142	100172
Tc58	5	0.4	0.35556	1	0	100172
Tc71	5	0.2	0.2	1	0	100172
SW_3						
Tcri13	4	1	0.82143	0.76785	0.00126	100172
Tcri27	4	0.75	0.67857	1	0	100172
Tcri36	4	0.75	0.85714	0.66084	0.00138	100172
Tcri35	4	0.75	0.89286	0.4571	0.00196	100172
Tcri29	4	1	0.78571	1	0	100172
Tcri46	3	0.66667	0.8	0.61006	0.00145	100172
Tc68b	4	1	0.89286	1	0	100172
Tc66	4	0.25	0.25	1	0	100172
Tc81	4	1	0.67857	0.31752	0.00135	100172
Tc52	4	0.5	0.75	0.32038	0.00156	100172
Tc70	4	0.75	0.53571	1	0	100172
Tc50	4	1	0.96429	1	0	100172
Tc74	4	0.5	0.82143	0.30849	0.00136	100172
Tc85	4	0.25	0.25	1	0	100172
Tc69	4	1	0.57143	0.31713	0.00153	100172
Tc58	4	0.25	0.25	1	0	100172

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Tc71	4	0	0.42857	0.14226	0.00114	100172
SW_4						
Tcri13	24	0.79167	0.78369	0.72846	0.00115	100172
Tcri27	24	0.91667	0.83777	0.78172	0.00096	100172
Tcri36	24	0.91667	0.91312	0.69026	0.00086	100172
Tcri35	24	0.75	0.83422	0.58068	0.00117	100172
Tcri29	24	0.75	0.73138	0.87184	0.00076	100172
Tcri46	24	0.79167	0.82801	0.19264	0.00126	100172
Tc68b	24	0.91667	0.85284	0.88386	0.00086	100172
Tc66	24	0.66667	0.73227	0.66966	0.00127	100172
Tc81	24	0.45833	0.60372	0.04463	0.00074	100172
Tc52	24	0.54167	0.53014	0.7358	0.00126	100172
Tc70	24	0.54167	0.52926	1	0	100172
Tc50	24	0.875	0.92819	0.16215	0.0003	100172
Tc74	24	0.45833	0.62057	0.09004	0.00072	100172
Tc85		This locus in monomorphic: not test done				
Tc69	24	0.20833	0.23138	0.28957	0.00156	100172
Tc58	24	0.29167	0.32358	0.60174	0.00141	100172
Tc71	24	0.25	0.28369	0.50003	0.00167	100172
SW_5						
Tcri13	25	0.92	0.79347	0.12284	0.00118	100172
Tcri27	25	0.92	0.84571	0.54492	0.00138	100172
Tcri36	25	0.88	0.87184	0.81656	0.00074	100172
Tcri35	25	1	0.88653	0.53394	0.00129	100172
Tcri29	25	0.76	0.7698	0.46142	0.00087	100172
Tcri46	25	0.72	0.81551	0.15603	0.00078	100172
Tc68b	25	0.68	0.82204	0.34993	0.00114	100172
Tc66	25	0.44	0.60408	0.18357	0.00125	100172
Tc81	25	0.48	0.63184	0.11149	0.00079	100172
Tc52	25	0.48	0.54204	0.70841	0.00125	100172
Tc70	25	0.44	0.49714	0.68769	0.00147	100172
Tc50	25	1	0.93388	0.99629	0.00013	100172
Tc74	25	0.56	0.60327	0.43181	0.00158	100172
Tc85	25	0.08	0.07918	1	0	100172
Tc69	25	0.32	0.33388	1	0	100172
Tc58	25	0.36	0.40245	0.69829	0.00178	100172
Tc71	25	0.4	0.42449	0.39998	0.00125	100172
SW_6						

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Tcri13	70	0.81429	0.78561	0.24307	0.00112	100172
Tcri27	71	0.8169	0.81251	0.51053	0.00126	100172
Tcri36	71	0.91549	0.89332	0.51332	0.00056	100172
Tcri35	71	0.88732	0.88573	0.23223	0.00135	100172
Tcri29	71	0.71831	0.74878	0.73377	0.00076	100172
Tcri46	71	0.74648	0.80951	0.57392	0.00228	100172
Tc68b	71	0.8169	0.83188	0.91901	0.00072	100172
Tc66	71	0.50704	0.55429	0.12247	0.00073	100172
Tc81	71	0.69014	0.64189	0.70026	0.00134	100172
Tc52	71	0.49296	0.50055	0.97727	0.00051	100172
Tc70	71	0.39437	0.53491	0.06897	0.00076	100172
Tc50	71	0.92958	0.93967	0.87074	0.00041	100172
Tc74	71	0.57746	0.64879	0.57154	0.00124	100172
Tc85	71	0.12676	0.12207	1	0	100172
Tc69	71	0.42254	0.40146	0.05835	0.00075	100172
Tc58	71	0.30986	0.32634	0.83009	0.00102	100172
Tc71	71	0.25352	0.31046	0.04087	0.00065	100172
SW_7						
Tcri13	33	0.84848	0.78928	0.54102	0.00175	100172
Tcri27	33	0.78788	0.83124	0.83317	0.00094	100172
Tcri36	33	0.9697	0.91608	0.60212	0.00089	100172
Tcri35	33	0.87879	0.85408	0.75686	0.00115	100172
Tcri29	33	0.72727	0.76643	0.69519	0.00153	100172
Tcri46	28	0.67857	0.76104	0.39961	0.00147	100172
Tc68b	32	0.71875	0.80853	0.47093	0.00115	100172
Tc66	32	0.71875	0.65179	0.52389	0.00155	100172
Tc81	33	0.75758	0.6331	0.60341	0.00189	100172
Tc52	33	0.51515	0.53939	0.32529	0.00147	100172
Tc70	33	0.45455	0.531	0.68641	0.00144	100172
Tc50	32	1	0.93601	0.95765	0.00033	100172
Tc74	33	0.75758	0.64429	0.26395	0.00096	100172
Tc85	33	0.12121	0.11748	1	0	100172
Tc69	33	0.39394	0.36317	1	0	100172
Tc58	33	0.24242	0.31142	0.16258	0.00106	100172
Tc71	33	0.54545	0.45361	0.67903	0.00133	100172
SW_8						
Tcri13	46	0.63043	0.75346	0.01423	0.00022	100172
Tcri27	46	0.82609	0.81558	0.49626	0.00116	100172

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Tcri36	46	0.8913	0.89059	0.20258	0.00077	100172
Tcri35	46	0.91304	0.86789	0.00566*	0.00019	100172
Tcri29	46	0.71739	0.75538	0.66896	0.00139	100172
Tcri46	39	0.76923	0.77423	0.22925	0.00094	100172
Tc68b	45	0.84444	0.83895	0.9837	0.00038	100172
Tc66	44	0.54545	0.61599	0.28708	0.00123	100172
Tc81	46	0.69565	0.62112	0.24812	0.00125	100172
Tc52	46	0.52174	0.44147	0.45704	0.00135	100172
Tc70	46	0.43478	0.48017	0.44641	0.00126	100172
Tc50	44	0.93182	0.9232	0.10037	0.00033	100172
Tc74	46	0.58696	0.57167	0.18246	0.00104	100172
Tc85	45	0.04444	0.04419	1	0	100172
Tc69	46	0.23913	0.24534	1	0	100172
Tc58	46	0.36957	0.41113	0.69973	0.00142	100172
Tc71	45	0.48889	0.42772	0.4322	0.00125	100172
SW_9						
Tcri13	18	0.88889	0.76032	0.71028	0.00141	100172
Tcri27	18	0.88889	0.77937	0.54264	0.00055	100172
Tcri36	18	0.94444	0.8873	0.85888	0.00068	100172
Tcri35	18	0.88889	0.87302	0.64297	0.00114	100172
Tcri29	18	0.83333	0.75397	0.52409	0.00126	100172
Tcri46	17	0.64706	0.62032	0.87773	0.00096	100172
Tc68b	17	0.94118	0.84314	0.43136	0.00113	100172
Tc66	18	0.33333	0.47937	0.21932	0.00096	100172
Tc81	18	0.61111	0.63016	0.77928	0.00122	100172
Tc52	18	0.44444	0.55714	0.0534	0.00069	100172
Tc70	18	0.38889	0.53175	0.21863	0.00133	100172
Tc50	18	0.88889	0.93651	0.7629	0.00055	100172
Tc74	18	0.72222	0.56667	0.23165	0.00135	100172
Tc85	18	0.16667	0.16032	1	0	100172
Tc69	18	0.38889	0.3381	1	0	100172
Tc58	18	0.27778	0.33175	0.51617	0.00162	100172
Tc71	18	0.27778	0.25238	1	0	100172
SW_11		Only one sampled individual				

Results are presented for the number of tested genotypes (#Genot) per locus, the observed (H_o) and the expected heterozygosity (H_e), the probability of deviation (p) with standard deviation (SD) and the number of steps of the chain (Steps done). Significant deviations after Bonferroni ($p<0.002$) are indicated in bold, a trend ($p<0.01$) is indicated with an asterisk.

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Table S6. Significant Linkage Disequilibrium (significance level=0.05) between pairs of loci at the a) regional level; b) SSP level.

a)

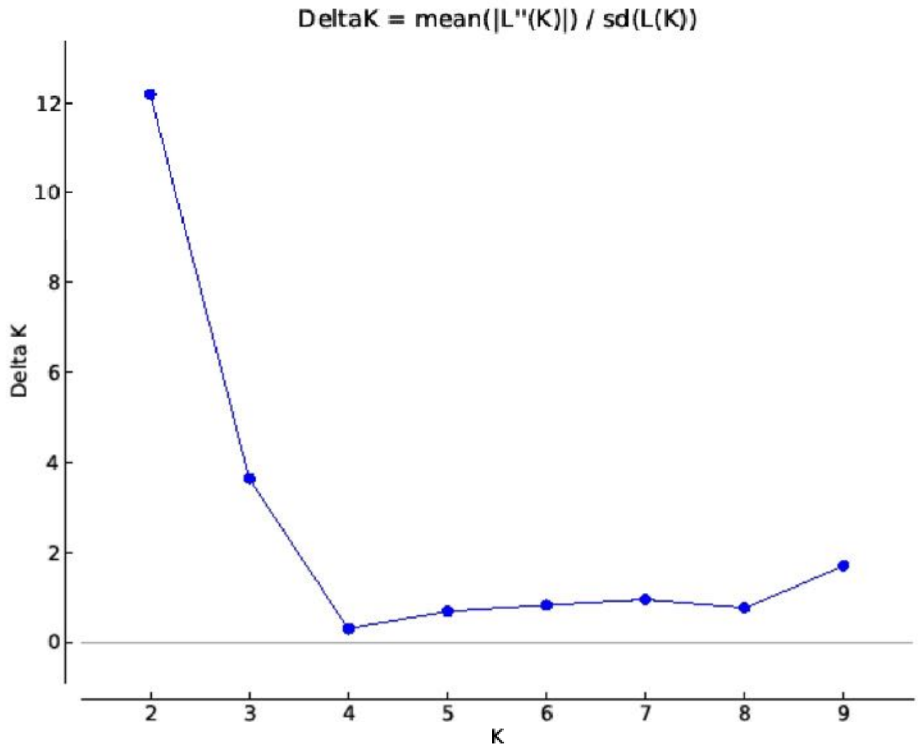
	Tcri 13	Tcri 27	Tcri 36	Tcri 35	Tcri 29	Tcri 46	Tc 68b	Tc 66	Tc 81	Tc 52	Tc 70	Tc 50	Tc 74	Tc 85	Tc 69	Tc 58	Tc 71
Tcri13																	
Tcri27	2																
Tcri36	3	2															
Tcri35	1	1	1														
Tcri29		1	1														
Tcri46	2	2	2	4	1												
Tc68b			1		1	1											
Tc66	1			1		1	2										
Tc81						1		1									
Tc52	2						2										
Tc70									1								
Tc50	1	2	6	1			1	1			1						
Tc74		2				1		1	1								
Tc85						1			2	1		2					
Tc69						1				1	1						
Tc58			1				5			1					1		
Tc71										1	1				1		

b)

	Tcri 13	Tcri 27	Tcri 36	Tcri 35	Tcri 29	Tcri 46	Tc 68b	Tc 66	Tc 81	Tc 52	Tc 70	Tc 50	Tc 74	Tc 85	Tc 69	Tc 58	Tc 71
Tcri13																	
Tcri27	1																
Tcri36	1	5															
Tcri35	2	2	3														
Tcri29	1	2	3	3													
Tcri46	2	2	4	1	2												
Tc68b		1	3	1	1	2											
Tc66	2	1	1	2			3										
Tc81	1	3	3	1	1	2	2	2									
Tc52	2			2			2	3	3								
Tc70		1	3		2		1	1	1	2							
Tc50	1	1	13	1		4	4	4	2	1	2						
Tc74	1	4	2	2	2	2	3	3	2		1	1					
Tc85				1		1	1		2	1	1	1					
Tc69	2	2	2	2		2	2	1		1		2	2	1			
Tc58	1	1	1		1	1	7		1	1	1	1	1	1	3		
Tc71	2	2	1	1		4	1	1	1				3	1	4	2	

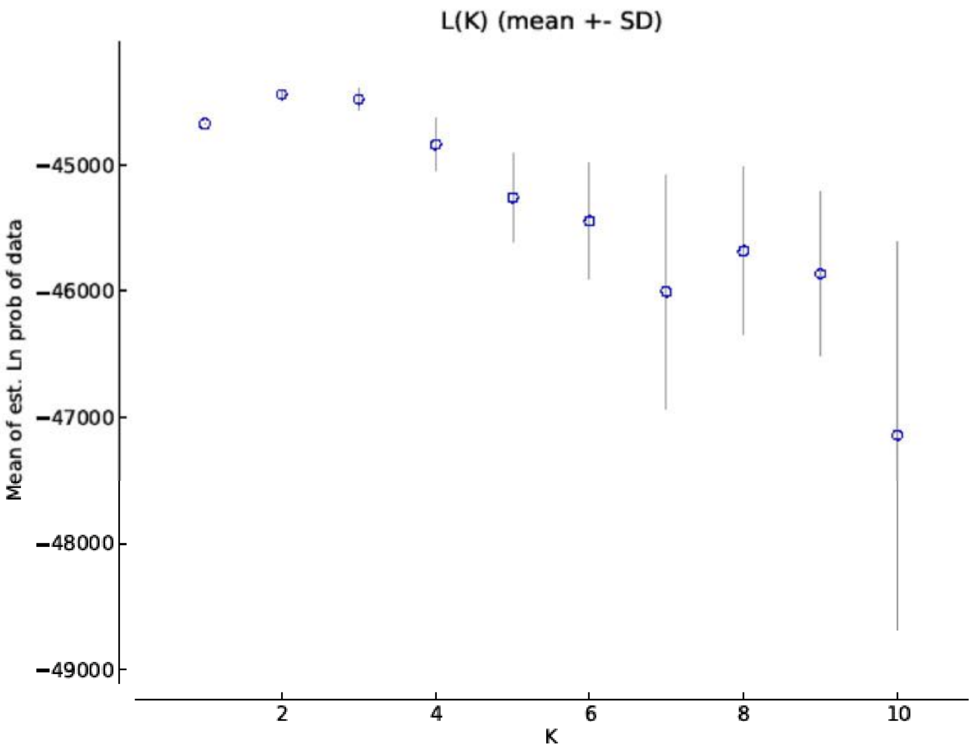
Indicated is the number of ponds (shown in different colors) in which the loci are linked.

Figure S1: Delta *k* values over ten runs for each *K* for the STRUCTURE analysis of 25 ponds at the SSP level using the Evanno method implemented in program STRUCTURE HARVESTER.



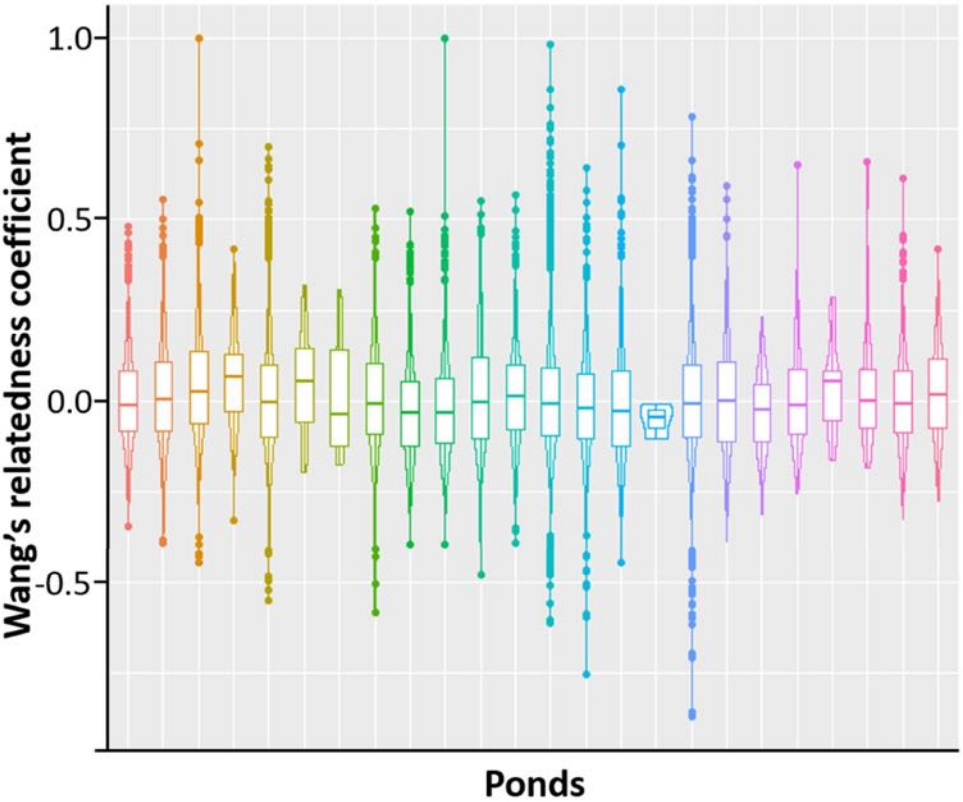
MOLECULAR ECOLOGY

Figure S2: Mean L(K) and SD over ten runs for each *K* from 1 to 10 obtained by STRUCTURE HARVESTER to achieve the most likely number of distinct genetic clusters of 25 ponds at the SSP level.



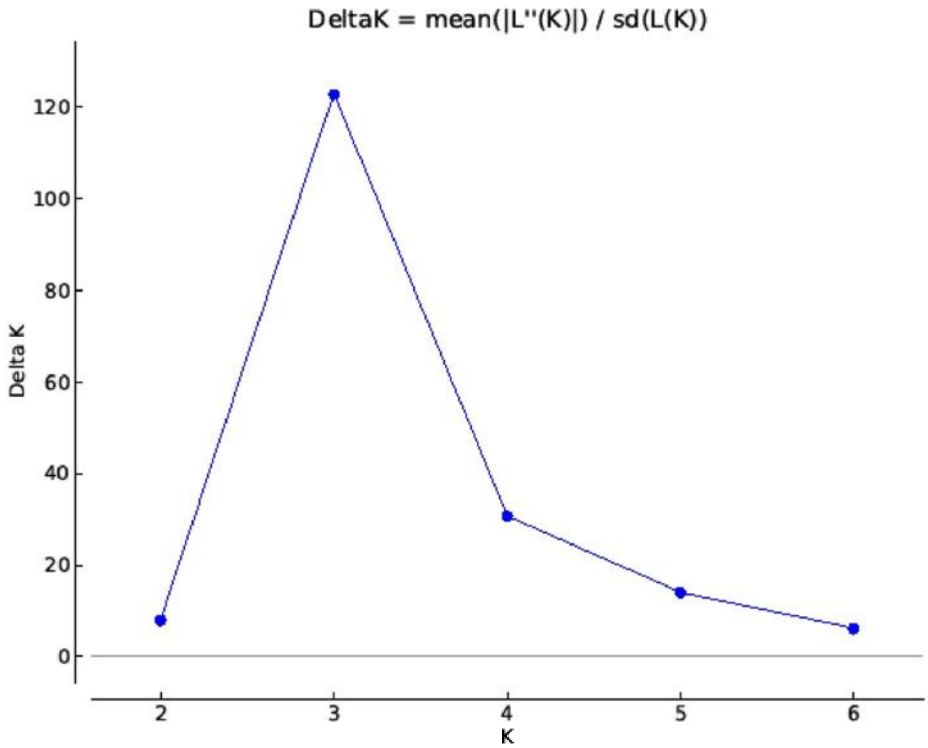
MOLECULAR ECOLOGY

Figure S3. Distribution of relatedness coefficients at 24 ponds located within the SSP.



MOLECULAR ECOLOGY

Figure S4: Delta *k* values over ten runs for each *K* for the STRUCTURE analysis of seven sampling locations at the regional level using the Evanno method implemented in program STRUCTURE HARVESTER.



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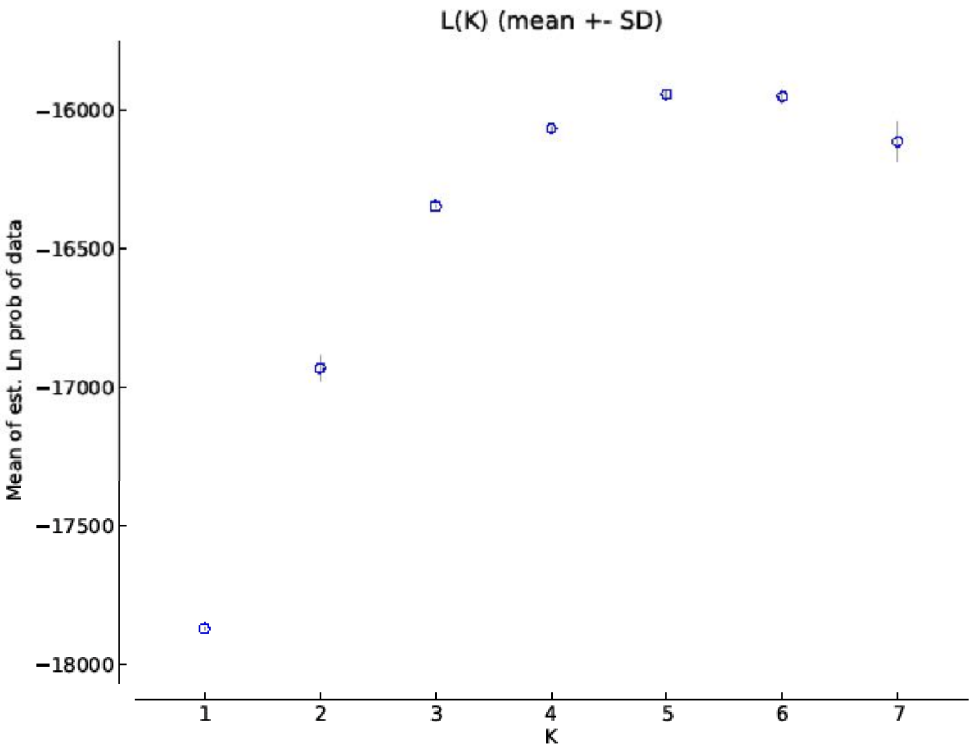
MOLECULAR ECOLOGY

Figure S5: Mean L(K) and SD over ten runs for each *K* from 1 to 7 obtained by STRUCTURE HARVESTER to achieve the most likely number of distinct genetic clusters of seven sampling locations at the regional level.



Chapter IV

Pond construction for amphibian conservation: phenotypic traits influence the colonization process

In preparation for submission

Lukas Diehl, Bianca Unglaub, Alexander Haas, Arlo Hinckley, Sebastian Steinfartz, Benedikt R. Schmidt

Pond construction for amphibian conservation: phenotypic traits influence the colonization process

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Abstract

Pond construction is considered an important conservation tool for threatened amphibian species to compensate for the ongoing degradation and loss of natural aquatic breeding habitats. Studying the effectiveness of such conservation actions and identifying factors influencing the colonization process may advance conservation practice substantially. Here, we used mark-recapture, phenotypic and genetic data to better understand the colonization process of constructed ponds for the Great Crested Newt (*Triturus cristatus*), an European amphibian species of high conservation concern. To support an existing pond network harbouring an extensive spatially structured newt population, 18 ponds have been constructed concurrently within a nature reserve in Northern Germany. We analysed the spatiotemporal pattern of colonization during the first three years, determined dispersal distances of colonizers and compared phenotypic traits of individuals captured in new and established ponds. Our study demonstrates that pond construction can be an effective conservation tool: new ponds were rapidly colonized and successful breeding was observed in half of the occupied ponds. Although short-distance movements prevailed among colonizers, they were predominantly not found in the closest new pond, suggesting that amphibians adjust their dispersal decisions according to local fitness prospects. The results of this study are discussed with regard to implications for conservation management. In addition, our study shows that phenotypic traits related to dispersal (i.e. age, body size, and body condition) can affect colonization ability: newts captured in new ponds were younger and tended to be larger than those in established ponds, indicating that colonization is mostly the result of natal dispersal by large individuals. While females in new ponds had a higher body condition than those in established ponds, the opposite was true for males, suggesting sex differences in dispersal syndromes.

Keywords: *Triturus cristatus*, dispersal syndrome, phenotype-dependent dispersal, conservation success, pond network

Introduction

Given the rapid loss of biodiversity, there is an urgent need for the systematic assessment of the outcomes of conservation actions in order to improve their effectiveness and to base future conservation strategies and recommendations upon experience and evidence rather than upon anecdotal sources (Semlitsch, 2002; Sutherland et al., 2004; Ceballos et al. 2017; Schmidt et al., 2019). Amphibians are globally recognized as the vertebrate group most threatened with extinction (Houlahan et al., 2000; Stuart et al., 2004; Beebee & Griffiths, 2005). One of the primary causes of the global amphibian decline is habitat degradation or destruction, particularly through the loss of breeding ponds (Baker & Halliday, 1999; Magnus & Rannap, 1999). Over the past century, many ponds have disappeared and those remaining have often lost quality, affecting the overall connectivity of amphibian populations (Rannap et al., 2009; Arntzen et al., 2017). These ponds are not only of extreme value for amphibian populations but also contribute significantly to aquatic biodiversity in terms of their species richness and species rarity (Williams et al., 2003; Davies et al., 2008). In order to compensate for the degradation and loss of natural aquatic habitats, amphibian conservation projects and wetland management plans often include the restoration and creation of ponds. The study of the effectiveness of such conservation actions holds the potential to advance conservation practice substantially (Schmidt et al., 2019).

Pond construction or restoration projects for amphibians are commonly viewed as successful if species of conservation concern colonize and reproduce in restored or newly created ponds (Baker & Halliday, 1999; Calhoun et al., 2014). It is therefore necessary to conceive the factors that determine colonization processes. Previous studies found ample evidence that pond characteristics (Rannap et al., 2009; Ruhi et al., 2012; Hossack, 2017) and the surrounding landscape (Stumpel & van der Voet, 1998; Shulse et al., 2010, Magnus & Rannap 2019) affect the colonization of ponds. The distance to potential source populations as well as connectivity were shown to be important factors influencing occupancy probability (Sjögren-Gulve, 1994; Baker & Halliday, 1999; Heard et al., 2012; O'Brien et al., 2021).

While habitat and landscape characteristics as well as the distances between newly created and established ponds are certainly important for the colonization of new ponds, we believe that it is worthwhile to study additional components of the colonization process. Colonization is a process whereby individuals disperse to and become established in new areas of currently uninhabited, suitable habitat. Dispersal of individuals appears to be an active process rather than simple passive diffusion and can be considered as a three-stage process including departure from the site of origin, transience in the landscape matrix und finally settlement at a new site (Clobert et al., 2009). Phenotypic traits such as morphology, physiology and behaviour influence each stage of the dispersal process (Bowler & Benton, 2005; Clobert et al., 2009; Cote et al., 2017), leading to dispersal syndromes (Ronce & Clobert, 2012). Several studies found phenotypic differences between dispersers and philopatric individuals in amphibians (e.g. Holenweg-Peter, 2001; Lowe & McPeek, 2002; Denoël et al., 2018). Phenotypic traits related to dispersal may also be important drivers of colonization success and the phenotypic composition of populations in newly created and established habitats may therefore differ from one another (Clobert et al., 2009).

In this study, we used mark-recapture, phenotypic and genetic data to better understand the colonization process in a European flagship species for amphibian conservation, the Great Crested Newt (*Triturus cristatus*). The data were collected in a nature reserve where a large number of ponds was constructed during winter 2011/2012 to support an existing network of ponds harbouring an extensive spatially structured population of *T. cristatus* (Unglaub et al., 2018; Unglaub et al., 2021). First, we analysed the spatiotemporal pattern of colonization. The new ponds in our study area met habitat requirements of pond-breeding amphibians and were situated at small distances to existing ponds. We therefore expected that new ponds should be colonized quickly after construction (Arntzen & Teunis, 1993; O'Brien et al. 2021). However, since successful reproduction depends on higher habitat quality than mere species presence in crested newts (Unglaub et al., 2021), the arrival of colonizers may not always result in the emergence of larvae. Second, we used mark-recapture data to investigate where the colonizers come from and what distances they have covered before immigration. Furthermore, we used genetic data to analyse population differentiation between new ponds and to test for isolation by distance (IBD). Since amphibians are considered to constitute poor dispersers and since their dispersal curves are dominated by short movements (Smith & Green, 2005), we expected that short-distance dispersal should prevail among colonizers, but that occasional long-distance dispersal may occur. Consequently, we assumed that genetic differentiation between new ponds should increase with increasing distance. Third, we applied phenotypic data to compare body size, body condition and age of newts captured in new and established ponds. Since dispersal capacity and propensity is usually positively affected by body size (Beck & Congdon, 2000; Denoël et al., 2018; Cayuela et al., 2020b), we expected colonizers captured in new ponds to be larger than individuals found in established ponds. Since dispersal involves a variety of costs during transience and at settlement and since higher body condition can mitigate these costs, we expected colonizers to be fatter (Clobert et al., 2009). Assuming that most dispersal occurs during the juvenile phase (Berven & Grudzien, 1990; Pittman et al., 2014), we expected newts in new ponds to be younger than those in established ponds.

Methods

Study species

With its biphasic life cycle, *T. cristatus* has distinct habitat requirements for both the aquatic and the surrounding terrestrial habitat (Ringsby et al., 2006; Gustafson et al., 2011). Crested newts remain in ponds until metamorphosis (larval stage) and during breeding once they become mature, whereas they usually remain terrestrially close to ponds at the juvenile stage and after a breeding event (Jehle, 2000; Jarvis, 2016). *T. cristatus* reaches sexual maturity at the age of 2-3 years (Miaud & Castanet, 1993). Although a life expectancy of 14 and 16 years was recorded for males and females respectively, the distribution mode was 3 years with a fast drop of older individuals in a pond network in France (Miaud & Castanet, 1993). The Great Crested Newt is an important key species for wetland conservation (O'Brien et al., 2015). *T. cristatus* is listed in Annexes II and IV of the European Habitats-Directive (92/43/EEC) and EU member states are required to monitor the conservation status of the species.

Study area

The two adjacent nature reserves "Höltigbaum", a former military training area, and "Stellmoorer Tunneltal" are located in the northeast of Hamburg, Germany (53.6125366 N, 10.1770651 E, 33 m asl). Mainly due to its remarkably large population of crested newts, the site (743 ha in size) is designated as special area of conservation under the Habitats Directive since 2004. The hilly landscape is very heterogeneous with open grassland, deciduous forests, shrubs, small water bodies, swamp forests and reeds. German heath, other sheep breeds and Galloway cattle are used for conservation grazing in the area. A railway line cuts through the nature reserve and its boundaries are weakened by human settlements and roads.

Around the turn of the year 2011/2012, 18 ponds were newly constructed in order to strengthen and expand the existing network of ponds (Figure 1). New ponds had an average size of 304 (± 126) m^2 and an average depth of 1 (± 0.45) m. The both outermost ponds within the study area are located 3923 m away from each other. The mean distance from a newly created pond to the nearest established pond is 273 m, ranging from 71 m to 489 m.

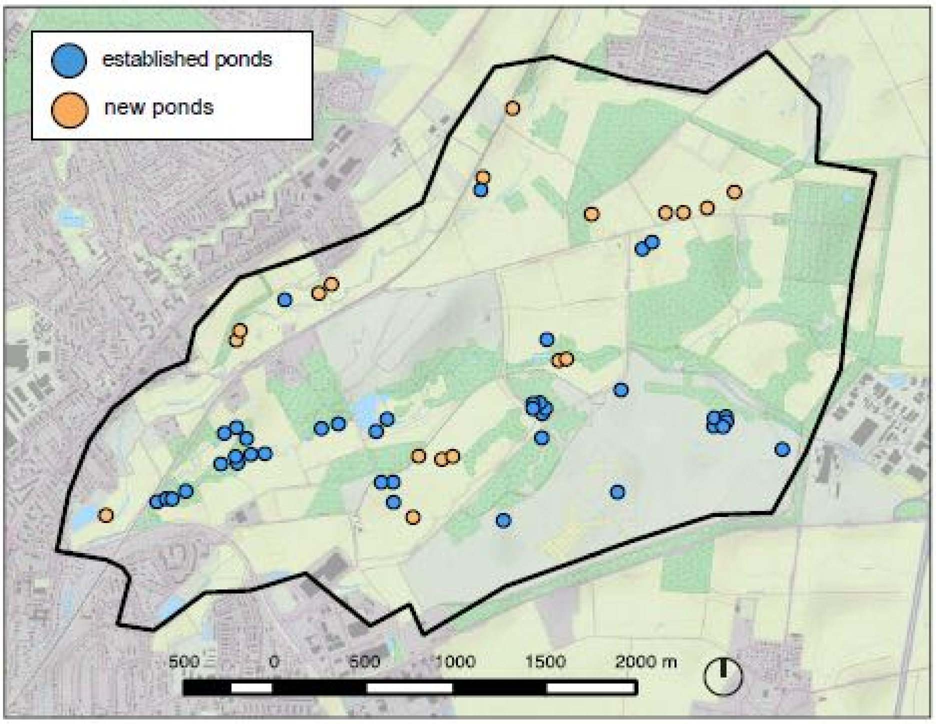

Figure 1: Location of established (blue dots) and new ponds (orange dots) within the study area in the northeast of Hamburg, Germany. The map was created using QGIS version 2.8 (www.qgis.org).

Mark recapture survey

In the course of a capture-mark-recapture study between 2012 and 2014, we surveyed 33 established and 18 newly created ponds for the presence and reproduction of *T. cristatus*. Ponds were visited 7-10 times per breeding season and newts were captured using Ortmann's funnel traps (Drechsler et al., 2010). Traps were evenly distributed along the shoreline and remained in the water for 48 hours. During the 2012 breeding season, only 3 of the new ponds were already filled with water, while in 2013 only 14 new ponds could be visited due to logistical limitations. In 2014, all new ponds (except one which remained dry that year) were surveyed for crested newts. Given this survey design, we could not use multistate mark-recapture models to estimate movement rates. Instead, we provide descriptive statistics of the observed movements between ponds.

For individual recognition, we photographed the ventral side of newts which shows a highly variable but individually unique and stable colour pattern. Recaptured individuals were identified using the software AMPHIDENT (Matthé et al., 2017). Individuals captured in different ponds constitute direct evidence of dispersal. Detected movements between ponds were categorized as i) dispersal between established ponds and ii) colonization events (i.e. dispersal from established to new pond).

Phenotypic traits

The snout-vent length (SVL) of 3206 captured newts was measured with a ruler to the nearest 0.1 cm. A two-way ANOVA (pond type x sex) was used to test whether the SVL of newts differ between established and new ponds. Body size distributions (i.e. SVL) of adult newts were displayed for both pond types and sexes separately.

For the calculation of a body condition index, the body mass (m) of each individual was measured with a portable micro scale to the nearest 0.1 g. After $\log_{10}$-transformation of the data, body mass was regressed on body size and the residuals of this regression were used as residual condition index R_i. To test whether body condition differs between new and established ponds, one-way Kruskal-Wallis analyses between the pond types were performed for males, females and juveniles.

Skeletochronology was used to compare the age of newts captured in new and established ponds. Age determination is based on the number of lines of arrested growth (LAGs) in the phalanges and is a reliable measure of age in short-lived animals such as *T. cristatus* (Sinsch, 2015). LAGs are annual growth rings formed in bones due to the annual cycle of increased (during spring and summer) and decreased activity (during autumn and winter). Age was estimated for a subset of individuals (new ponds: n = 131; established ponds: n = 154; for a detailed description of the procedure see Unglaub et al., 2018). The age of captured newts was compared between pond types (established vs. new) and between sexes (males vs. females) using a Poisson regression. The pond ID was added to the model as random factor. Subsequently, age was correlated with the residual condition index (R_i) and with body size (SVL).

DNA extraction and microsatellite analysis

1500 tissue samples (established ponds: n = 981; new ponds: n = 519) were taken by puncturing the tails of newts using micro haematocrit capillary tubes (Carl Roth, Ø 1.6 mm). Tissue samples were then stored in 80% ethanol. Total genomic DNA was extracted using the sodium dodecyl sulfate (SDS)-proteinase K/ Phenol-Chloroform extraction method. The DNA was then stored in Tris-EDTA buffer (10 mM Tris-HCl, 0.1 mM EDTA, pH 8.0) and used for all subsequent reactions. A gel electrophoresis showed high concentration of DNA in the samples.

Each individual sample was genotyped for 17 highly polymorphic microsatellite loci (see Drechsler et al., 2013 and Unglaub et al., 2021 for more details). Microsatellite analysis was performed using GENEMARKER software (SoftGenetics version 1.95). The data were tested for null alleles with the software MICRO-CHECKER (van Oosterhout et al., 2004).

Population structure and isolation by distance

In order to infer the population structure, a model-based Bayesian clustering method was performed using the software STRUCTURE (version 2.3.4.; Pritchard et al., 2000). We used the admixture model without local prior and a burn-in period of 20000 Markov chain Monte Carlo (MCMC) iterations, followed by 50000 iterations for k=1 through k=8 with 10 replicates for each k. The software STRUCTURE HARVESTER (Earl, 2012) was used to obtain the most likely number of distinct genetic clusters using the Pr(D/K) method (Pritchard et al., 2000; Meirmans, 2015).

STRUCTURE results were additionally tested by the computation of pairwise F_{ST} values using the software FSTAT (version 2.9.3.2.). Differences of F_{ST} values between the three years of sampling can be neglected, because this time frame is shorter than the estimated generation time of the species (Jehle et al., 2005). In order to test for isolation by distance (IBD), the pairwise F_{ST} values and the geographic distance were correlated for 16 occupied new ponds using a Mantel test.

Results

Mark-recapture survey

In 2012, crested newts were captured in 2 out of 3 newly created ponds (67%) while this was the case in 12 out of 14 ponds (86%) in 2013. Since one of the new ponds was unavailable for colonization in 2014 (pond U remained dry throughout the season), the colonization rate within three breeding seasons after construction was 94% (i.e. 16 out of 17 available ponds were colonized). As none of the new ponds became unoccupied after being colonized the years before, the extinction rate was 0%. The occupancy rates of new ponds were comparable or even higher than those of established ponds (67%, 79% and 76% in the respective years).

While in 2012 only 18 adult crested newts were captured in the new ponds, we already found 152 individuals (adults and juveniles) in 2013 and 431 newts in 2014 (Figure 2). In the first season after construction, mainly males (61%) were captured in the new ponds, whereas females (73%) predominated in the second season. In the third season, the sex ratio was balanced (49% and 51% for males and females, respectively; Table 1). Post-metamorphic juveniles were also captured in the new ponds, although in smaller numbers than adults (Table 1). Adult crested newts used the new ponds not only as an occasion to forage but also for reproduction. Larvae were detected in about half of all occupied ponds, in some of them even in high numbers (Table 1).

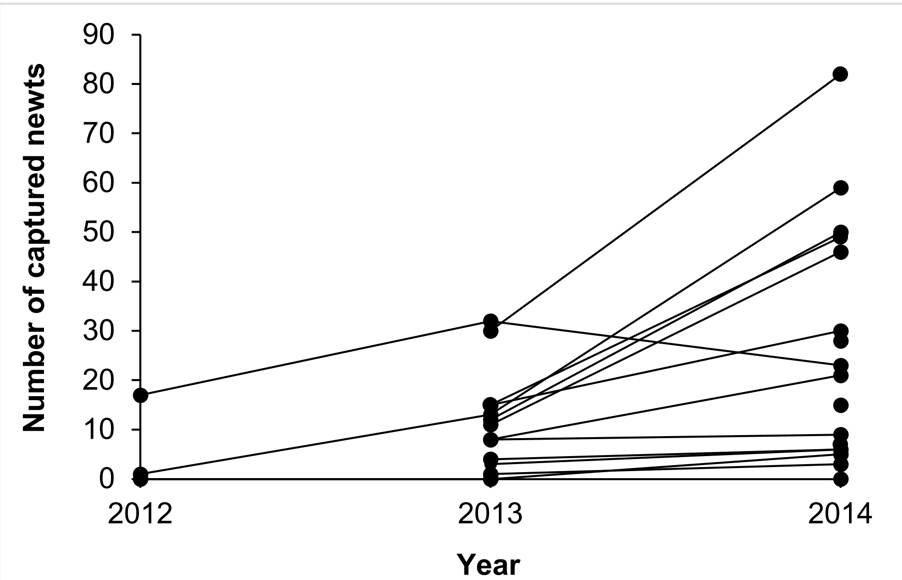

Figure 2: Positive colonization trend of the new ponds shown by an increasing number of captured *T. cristatus* in the first three years after construction (winter 2011/2012). Black dots represent the number of adult and juvenile newts captured in one specific pond.

Table 1: Number of captured *T. cristatus* per pond in the first three years of the colonization process. Number of larvae is given as maximum number of larvae captured at a single survey day. In 2012, only three ponds were already filled with water. In 2013, 4 ponds were not surveyed. In 2014, 1 pond remained dry throughout the season. % of ponds: Percentage of surveyed ponds where the different life stages of crested newts were captured in. M: Males, F: Females; J: Juveniles; L: Larvae.

	2012				2013				2014			
Pond	**M**	**F**	**J**	**L**	**M**	**F**	**J**	**L**	**M**	**F**	**J**	**L**
A					3	23	4	2	17	37	28	0
B					3	11	1	5	16	24	9	4
C					0	7	1	0	2	11	8	20
D					1	13	1	0	2	15	13	38
E	10	7	0	33	10	20	2	11	12	11	0	0
F					N/A	N/A	N/A	N/A	22	5	1	0
G	0	0	0	0	0	0	0	0	1	1	3	1
H	1	0	0	0	8	3	2	4	31	15	13	20
K					N/A	N/A	N/A	N/A	9	4	2	0
L					N/A	N/A	N/A	N/A	3	2	2	0
M					N/A	N/A	N/A	N/A	0	0	0	0
N					0	2	1	0	1	3	2	0
O					0	0	1	0	0	1	2	0
P					1	3	0	1	0	6	0	2
R					5	7	0	20	27	17	6	8
S					6	5	0	6	22	16	8	1
T					0	8	0	0	1	3	5	0
U					0	0	0	0	*Dried-up*			
∑	**11**	**7**	**0**	**33**	**37**	**102**	**13**	**49**	**166**	**171**	**102**	**94**
% of ponds	**67**	**33**	**0**	**33**	**57**	**79**	**57**	**50**	**82**	**94**	**82**	**47**

Dispersal events between ponds detected by the mark-recapture approach were categorized as either dispersal between established ponds (n = 227) or colonization of new ponds (n = 15). 14 newts colonized new ponds situated less than 500 m from their source pond (i.e. the established pond where they were previously captured in). However, 1 adult male dispersed further than 1000 m, thereby providing direct evidence of long-distance dispersal. 9 colonizers did not use the next closest located pond as destination. Observed dispersal between established ponds was also dominated by short-distance movements (95% of dispersal distances < 500m), whereas long-distance dispersal was scarce (0.9% of dispersal distances > 1000m; Figure 3).

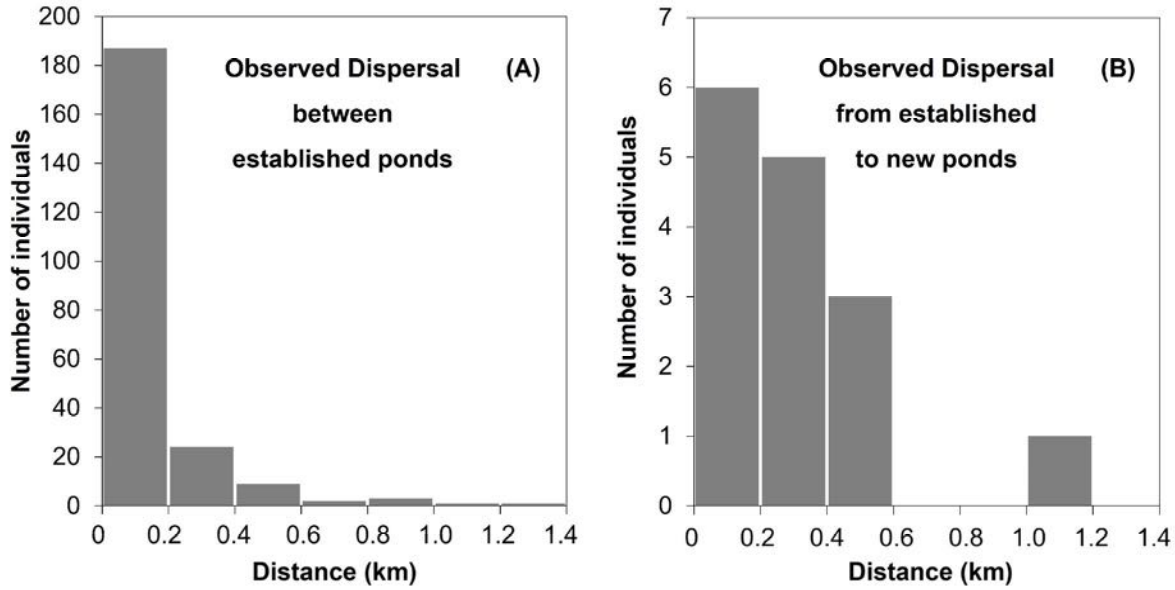

Figure 3: Frequency of dispersal events per distance category. Observed dispersal (A) between established ponds and (B) from established to new ponds (colonization).

Phenotypic traits

The body size of newts differed between new and established ponds (Figure 4; ANOVA, $F = 9.26$, $p = 0.002$) with an interaction effect of sex ($F= 3.19$, $p < 0.05$). Females, males and juveniles tended to be larger in new ponds than in established ones. However, this difference was only significant for females (Tukey test, $p < 0.001$).

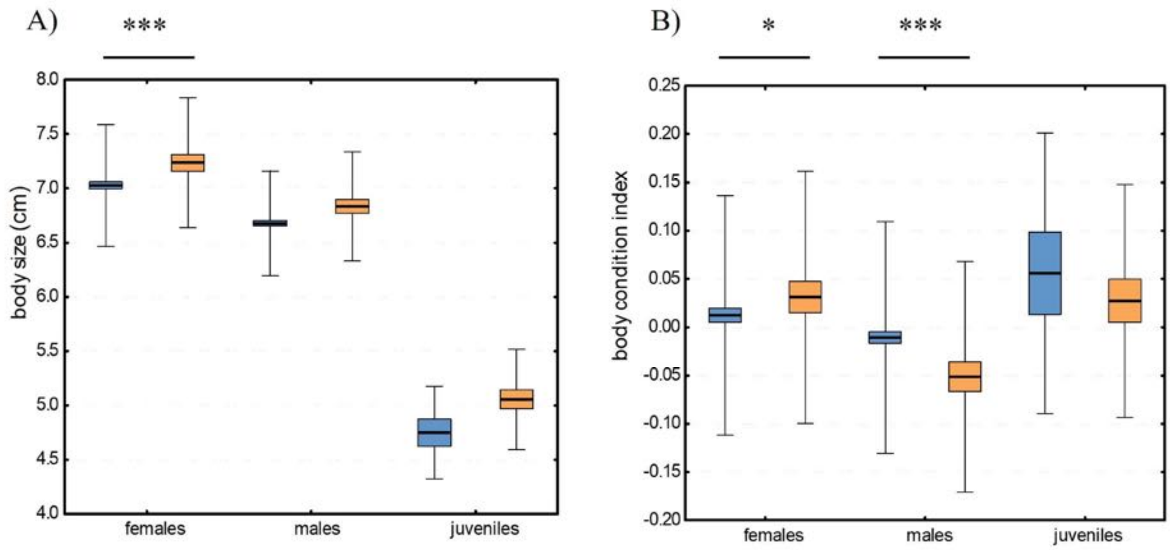

Figure 4: Differences in mean body size (SVL) and mean body condition (Ri) of *T. cristatus* in established (blue) and new ponds (orange). Asterisks indicate significant differences at different levels: * $p < 0.05$, *** $p < 0.001$. A) Females were larger in new ponds than in established ponds. B) Females had a higher body condition, whereas males had a lower body condition in new ponds.

In addition to differences in mean body size, we also observed differences in size distributions between new and established ponds. While the SVL was normally distributed in established ponds (skewness coefficient ≈ 0), the body size distribution was skewed to the left in new ponds (negative skewness coefficients), indicating that more individuals are larger than the mean value (Figure 5). This pattern was especially pronounced in females.

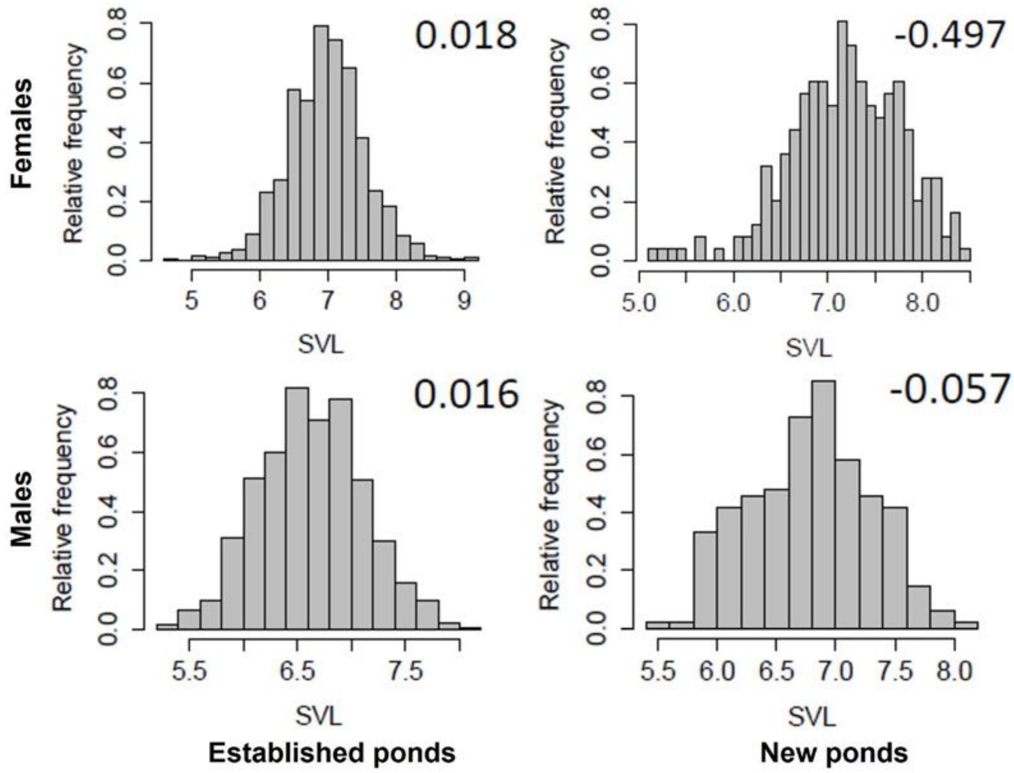

Figure 5: Size distribution histograms of female and male *T. cristatus* in established and new ponds. The skewness coefficient is given as measure of asymmetry.

Females in the new ponds had a significantly higher body condition than those in established ponds (Kruskal-Wallis test, $chi^2 = 4.4$, $p < 0.05$), whereas males had a much lower body condition in new ponds as compared to established ones (Figure 4, Kruskal-Wallis test, $chi^2 = 22.3$, $p < 0.001$). Juveniles did not differ significantly in body condition between the two pond types.

The skeletochronological analysis revealed that newts were younger (mean ± SE = 2.53 ± 0.12, n = 130) in new ponds than in established ones (mean ± SE = 3.18 ± 0.09, n = 153; Figure 6). This age difference was particularly pronounced in male newts. The number of LAGs did not correlate with the condition index, but with body size. The majority of the examined individuals were 2 or 3 years old (55% and 64% in new and established ponds, respectively). While 26% of all individuals were 1-year-old juveniles in the new ponds, this age class accounted for only 3% in the established ponds. By contrast, experienced breeders (individuals that are at least 4 years old) made up 19% in the new ponds but accounted for 33% of all individuals in the established ponds.

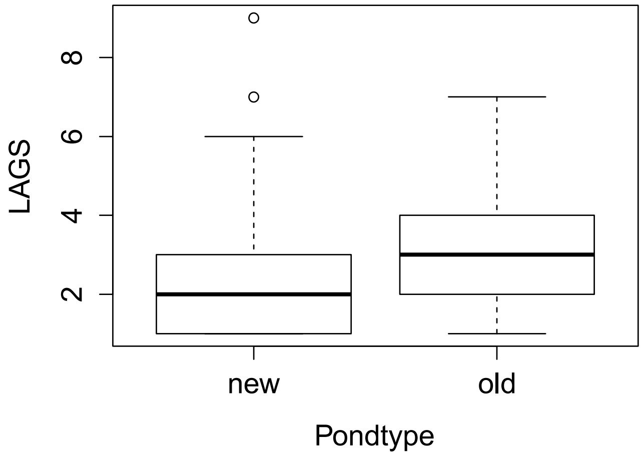

Figure 6: Number of LAGs (lines of arrested growth) for individuals in the new (n = 130) and in the established ponds (n = 153). Individuals in new ponds were significantly younger.

Genetic structure and isolation by distance

The genetic clustering analysis using the software STRUCTURE indicated the existence of two different genetic clusters within the spatially structured population of crested newts (Figure 7). While one genetic cluster was located in the southwestern part of the nature reserve, the other one was situated in the northeastern part of the study area. This result confirms previous analyses (see Unglaub et al., 2021) and reveals that the recently founded demes reflect the genetic structure of the study area.

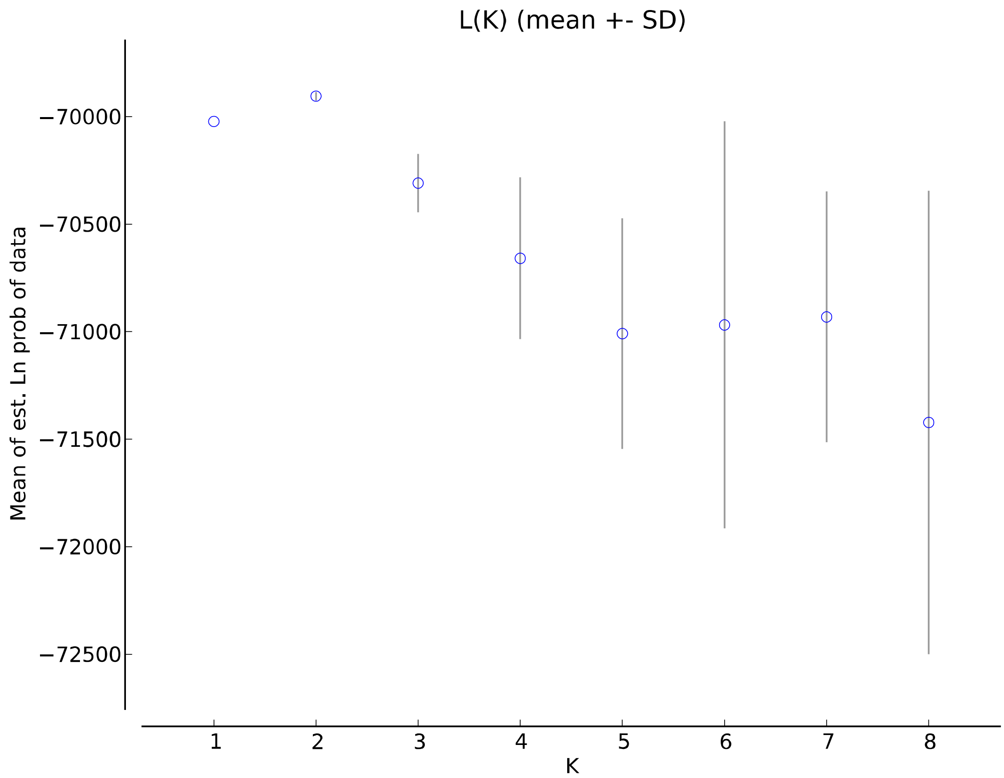

Figure 7: Mean L(K) and SD over ten runs for each K from 1 to 8 obtained by STRUCTURE HARVESTER to achieve the most likely number of distinct genetic clusters.

Further indication of significant genetic structure was given by testing for isolation by distance (IBD). The pairwise F_{ST} values between new ponds ranged from 0 to 0.03 and increased significantly with distance (Figure 8, Mantel test, $r = 0.26$, $t = 2.92$, $df = 118$, $p < 0.01$). This finding underlines that long-distance dispersal is rare compared to short-distance movements.

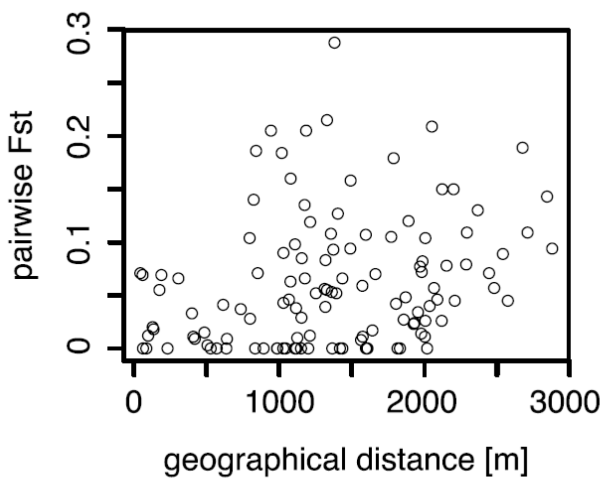

Figure 8: Isolation by distance (IBD) was significant (Mantel test: $p < 0.01$) for the new ponds as pairwise FST values between ponds increased with increasing distance. Only ponds where crested newts were captured in 2014 (16 out of 18) were included.

Discussion

We used mark-recapture, phenotypic and genetic data to better understand the colonization process of newly created ponds by an amphibian of European conservation concern, the Great Crested Newt. The network of 33 established and 18 new ponds surveyed in this study provided a rare opportunity to investigate dispersal in a quasi-experimental setting (Schmidt et al., 2019). *T. cristatus* colonized 16 out of 18 created ponds within the first three years after construction and breeding was successful in about half of all occupied ponds. Most colonizing events of newly created ponds occurred from established ponds in the proximity (< 500 m), still 9 out of 15 newts dispersed to new ponds more distant than the closest one available and one adult male dispersed further than 1000 m (long-distance dispersal). We found that newts captured in new ponds were younger and tended to be larger than those in established ponds. While females in new ponds had a higher body condition than those in established ponds, the opposite was true for males, indicating a sex difference in dispersal syndrome.

Spatiotemporal pattern of colonization

Our study shows that 94 % of the available new ponds were colonized within three years after construction (one pond remained dry in 2014 and thus was unavailable for colonization by crested newts) and that none of these populations went extinct during the observation period. This pattern is congruent with previous studies showing that crested newts are rapid colonizers who readily use restored or newly created ponds given the opportunity (Lenders, 1992; Arntzen & Teunis, 1993; O'Brien et al., 2021).

New ponds were not only colonized quickly but also quite frequently: the occupancy rates of new ponds (ranging from 67-94%) was comparable or even higher than the occupancy rates of established ponds (ranging from 67-76%). In contrast, Baker & Halliday, (1999) reported that *T. cristatus* occurred less frequently in newly created ponds as compared to established ones. However, they note that the new ponds in their study were primarily constructed for fish or waterfowl or for their aesthetic value. Conversely, Magnus and Rannap (2019) showed that crested newts occurred and reproduced considerably more often in ponds specifically constructed for threatened amphibian species rather than in natural ponds. They stress out that the presence and reproduction of *T. cristatus* was related to several landscape and pond characteristics (e.g. clear water, mineral sediment, absence of fish) which differed substantially between constructed and natural ponds.

Previous studies confirm that a high habitat suitability predicts abundance and reproductive success in crested newts (Unglaub et al, 2015; Unglaub et al., 2018). A higher habitat quality is needed for reproduction to occur rather than for mere species presence (Unglaub et al., 2021). In line with this, no larvae were detected in about half of the newly created ponds where adult newts were found. It is noteworthy that we found varying numbers of three-spined sticklebacks (*Gasterosteus aculeatus*) in 50% of these aforementioned ponds. Sticklebacks are small, predatory fish which can have serious impacts on crested newt larvae, probably through both predation and competition (Artnzen & Teunis, 1993; Oldham et al., 2000). Fish introductions are considered as a major threat for pond-breeding amphibians and can reduce or eliminate amphibian populations through predation, competition and even pathogen transfer (e.g. Hecnar & M'Closkey, 1997; Semlitsch, 2002; Kats & Ferrer, 2003; Hartel et al., 2007).

Dispersal distances of colonizers

The mark-recapture data revealed that most colonizers dispersed to new ponds located in the proximity of their established source pond. This pattern was equally confirmed by the genetic data which showed that population differentiation between new ponds increases with increasing geographic distance. Our findings are consistent with other recent research which found that pond colonization probability by crested newts decreases with increasing distance to the nearest occupied pond (O'Brien et al., 2021).

Although short-distance movements prevailed among colonizers (93% of dispersal distances < 500 m), we also found direct evidence for long-distance dispersal (max. distance travelled by a male: 1020 m). This result contradicts the findings of Baker & Halliday (1999) who showed that *T. cristatus* only colonized new ponds located within a distance of 400 m to existing ponds in an agricultural landscape in England. By contrast, O'Brien et al. (2021) found that crested newts colonized new ponds at distances up to 600m from established ponds in the Scottish Highlands. Variation in maximum dispersal distances between ponds observed in different study areas may be due to differences in the structure of the terrestrial habitat between ponds and the nature of the ponds themselves (Baker & Halliday, 1999). Moreover, there is accumulating evidence that high intra-specific variation in dispersal can result from both context- and phenotype-dependence of dispersal costs and benefits (Bowler & Benton, 2005; Clobert et al., 2009). Since the maximum dispersal distance for *T. cristatus* recorded so far is 1.650 m (Haubrock & Altrichter, 2017), even new ponds at distances of 1-2 km from the next source pond may get colonized (assuming no significant dispersal barriers in the intervening terrestrial habitat). To conclude, the dispersal pattern observed in our study is congruent with previous studies showing a leptokurtic distribution of movement distances in amphibians (Smith & Green, 2005; Lowe & McPeek, 2012; Hendrix et al., 2017; Cayuela et al., 2020b).

Curiously, 9 out of 15 colonizers detected by the mark-recapture approach were not found in the new pond which was closest to their source pond. However, in all these cases the closest new pond available was either pond A, pond E or pond T. Pond A was heavily used by the resident Galloway herd for drinking and chilling in the water. Cattle can destroy pond banks and aquatic vegetation by grazing and trampling and often increase nutrient load and turbidity (Schmutzer et al., 2008). Pond T was very shallow and dried towards the end of the breeding season. While occasional drying may have an overall beneficial effect by preventing fish colonization, pond desiccation before larval metamorphosis is completed will result in reproductive failure (Oldham et al., 2000; Semlitsch, 2002). In Pond E, we detected a growing number of sticklebacks since the end of the breeding season in 2013. Notably, we did not find larvae in any of these ponds in 2014 either. These findings suggest that colonizers may have avoided new ponds affected by grazing cattle, drying or fish introduction and rather dispersed to another one. This conclusion is supported by a growing number of studies showing that amphibians can adjust their dispersal decisions according to local fitness prospects of a patch (e.g. Joly, 2019; Cayuela et al., 2019; Cayuela et al., 2020b; Barille et al., 2021; Unglaub et al., 2021).

Phenotypic traits of colonizers

Our study indicates that phenotypic traits related to dispersal can affect colonization ability. The phenotypic composition of populations in recently colonized and established ponds differed from another noticeably. This result is consistent with previous studies showing phenotypic differences between dispersers and philopatric individuals in amphibians (e.g. Holenweg-Peter, 2001; Lowe & McPeek, 2002; Denoël et al., 2018).

First, crested newts tended to be larger in new ponds as compared to established ones. This difference was confirmed by the body size distribution of individuals which was skewed to the left in the new ponds, indicating a higher proportion of large individuals. This finding is consistent with other recent research that shows increasing breeding site infidelity (i.e. low site faithful phenotype) with increasing body size in *T. cristatus* (Denoël et al., 2018). In amphibians, body size usually has a positive influence on locomotion performance as measured by endurance and sprint speed and thus on dispersal capacity and propensity (Beck & Congdon, 2000; Denoël et al., 2018; Cayuela et al., 2020b). A larger body size may also reduce the mortality risk caused by dehydration during transience within the terrestrial landscape matrix (Hillman et al., 2009; Denoël et al., 2018). Finally, body size at metamorphosis is often positively correlated with exploration propensity, activity level and boldness in amphibians (Kelleher et al., 2018).

Second, while females showed a higher body condition in new ponds as compared to established ones, the opposite was true for males, indicating that dispersal decisions of males and females are differently affected by this trait. Dispersal is associated with a variety of costs (e.g. energy expenditure, increased mortality risk) but also augurs benefits (e.g. increased reproductive success, reduced intra-specific competition). The trade-off between costs and benefits of dispersal determines an individuals' propensity to disperse (Bowler & Benton, 2005) and can be influenced by the internal state of individuals (phenotype-dependence) as well as by external factors (context-dependence). Thus, individuals may differ in their motivation to emigrate from or to immigrate into a specific site (Cote et al., 2017). The body condition of an animal reflects its energy reserves and influences reproductive investment and fecundity (Reading & Clark, 1995; Scott & Fore, 1995; Cayuela et al., 2014). Individuals with higher body condition may have enough energy stores not only to offset energy expenditure during transience and settlement at an unfamiliar site but also to reproduce after dispersal. Given that the overall energy cost of reproduction is higher for female than for male crested newts (Cayuela et al., 2014; Cayuela et al., 2019), a higher body condition may positively impact emigration decisions of females in particular. In male crested newts, however, body condition has been shown to be positively correlated to crest and tail height (Baker, 1992) which in turn affect mating success (Hedlund, 1990). Male newts display territorial behaviour with temporal dominance hierarchies (Zuiderwijk et al., 1986; Jehle et al., 2011). Males with a lower body condition may therefore have a reduced likelihood of mating in established ponds with high male densities. Hence, a lower body condition may positively impact the decision of males to leave established ponds and to settle in new ponds with lower conspecific densities.

Third, newts captured in new ponds were younger than those in established ones, suggesting that colonization is mostly the result of natal dispersal. The majority of all individuals examined by skeletochronology were 2 or 3 years old in both new and established ponds (55% and 64%, respectively). This finding is consistent with Miaud and Castanet (1993) who reported a distribution mode of 3 years for a population of Great Crested Newts in a pond network in France. While 1-year-old juveniles represented a higher proportion of all individuals in the new ponds as compared to the established ones (26% and 3%, respectively), the opposite was true for experienced breeders (i.e. individuals ≥ 4 years old; 19% and 33%, respectively). Juveniles are widely regarded as primary dispersing life-stage in pond-breeding amphibian populations and consequently as life-stage mainly responsible for colonization events (Berven & Grudzien, 1990; Pittman et al., 2014). According to this assumption, the proportion of juveniles and young adults reproducing for their first time is expected to be particularly high in new ponds. The skeletochronological analysis generally confirmed this hypothesis (81% of colonizers were ≤ 3 years old). However, the age distribution showed that breeding dispersal also plays a significant role in the colonization process of new ponds (19% of colonizers were ≥ 4 years old). Several studies found higher rates of natal dispersal compared to breeding dispersal in amphibians (e.g. Berven & Grudzien, 1990; Sjögren-Gulve, 1998; Kupfer & Kneitz, 2000; Funk et al., 2005; Valenzuela-Sánchez et al., 2019), whereas other studies report similar rates of natal and breeding dispersal (e.g. Trenham et al., 2001; Smith & Green, 2006; Cayuela et al., 2020a). This variation in the respective proportions of natal and breeding dispersal may be context-dependent (Cayuela et al., 2020a).

Implications for conservation

Our study provides one of the few empirical cases demonstrating that the construction of new ponds can be an effective conservation tool to support existing pond networks harbouring spatially structured populations of threatened amphibian species. Almost all newly created ponds were rapidly colonized by *T. cristatus* and successful reproduction was observed in half of the occupied ponds. The presence of adults and larvae in a multitude of the new ponds suggests that new populations will establish there. However, it is important to keep in mind that with ongoing succession some of the populations may disappear after some years and that it may take five to ten years after pond construction until a reproducing population establishes at a pond (Semlitsch, 2002; Schmidt et al., 2019). Hence, we encourage long-term monitoring of new ponds in order to quantify occupancy and reproduction rates across time.

Our results corroborate the hypothesis that amphibians can adjust their dispersal decisions according to environmental cues and local fitness prospects (i.e. *informed dispersal*; Clobert et al., 2009). Colonizers probably avoided new ponds impacted by grazing cattle, pond drying or fish introduction and rather dispersed further distances to other ponds providing more attractive breeding habitat. In addition, successful reproduction was detected in none of these affected ponds. Therefore, management actions such as limiting livestock access to new ponds (by adding fences) or removal of fish populations may improve amphibian colonization of newly created ponds and thus the effectiveness of this conservation measure.

The mark-recapture and the genetic data equally showed that short-distance movements prevailed among colonizers. We therefore recommend that habitat creation projects for the conservation of pond-breeding amphibians should aim to create pond networks containing a variety of ponds arranged in clusters with relatively small inter-pond distances in order to facilitate dispersal (Rannap et al., 2009). Areas of higher pond density are not only of great value for amphibian diversity but also promote species richness and diversity of aquatic macroinvertebrate and macrophyte assemblages (Gledhill et al., 2008; Thiere et al., 2009).

Conclusion

Our results corroborate the view that dispersing individuals are not a random subset of the source population but differ in phenotypic traits from philopatric individuals (Bowler & Benton, 2005; Clobert et al., 2009; Cote et al., 2017). Crested newts captured in newly created ponds were younger and tended to be larger than those captured in established ponds, suggesting that colonization of new ponds is mostly the result of natal dispersal by large individuals. However, breeding dispersal likewise contributed to the colonization process and varying proportions of dispersal types may be context-dependent (Cayuela et al., 2020a). Notably, our analyses revealed that females in new ponds had a higher body condition as compared to established ponds, whereas the opposite was true for males, indicating that phenotypic traits may affect dispersal decisions of males and females in different ways. Therefore, our study contributes to the growing body of evidence for sex differences in dispersal syndromes (van Overveld, 2014; Legrand et al., 2016; Mishra et al., 2018).

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Author contributions

B.R.S. and S.S. designed the study. L.D. and B.U. conducted the field work. L.D., B.R.S. and B.U. performed the statistical analyses. A. Haas advised the technique of skeletochronology and A. Hinckley performed the work procedure. B.R.S., L.D. and B.U. wrote the manuscript.

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Talks

Unglaub, B., Cayuela, H., Schmidt, B. R., Preißler, K., Glos, J., Steinfartz, S. „Wählerische Wasserdrachen: ökologische und genetische Untersuchung einer räumlich strukturierten Kammmolch-Population". Herpetokolloquium der Info Fauna KARCH, Bern, Schweiz. Invited talk. December 2021

Unglaub, B. "Im Reich der Wasserdrachen". Infozentrum „Haus der Wilden Weiden" der Stiftung Natur im Norden, Hamburg, Germany. Invited talk. July 2015

Unglaub, B., Drechsler, A., Schmidt, B. R., Steinfartz, S. "Linking habitat suitability to demography: a case study on great crested newts (Triturus cristatus)". 107th Annual Meeting of the German Zoological Society, Göttingen, Germany. September 2014

Unglaub, B., Drechsler, A., Schmidt, B. R., Steinfartz, S. "Linking habitat suitability to demography in great crested newts (Triturus cristatus)". SEH 17th European Congress of Herpetology, Veszprem, Hungary. August 2013

Author contributions, Bianca Unglaub

The influence of habitat quality on demography, dispersal and population structure of great crested newts

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Author contributions:

Title: **Linking habitat suitability to demography in a pond-breeding amphibian**

Journal: Frontiers in Zoology

Authors: Bianca Unglaub, Sebastian Steinfartz, Axel Drechsler, Benedikt R. Schmidt

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Bianca Unglaub (first author): performed statistical analysis, wrote the manuscript

Sebastian Steinfartz (author 2): designed the study, provided input to the manuscript

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Benedikt R. Schmidt (senior author): designed the study, provided input to the manuscript

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Journal: Basic and Applied Ecology

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