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AQUATIC AND TERRESTRIAL HABITAT SELECTION BY AMPHIBIANS IN A DYNAMIC FLOODPLAIN

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This thesis is dedicated to the Tagliamento River,
the King of Alpine Rivers,
my wife Bea and daughter Lilly

The Flood

A toad
A fat toad
A croaking, fat toad
Hopping alongside the river

A blue river
A blue, clean river
A blue, clean river before the rain came

Torrential rain
Torrential, never ending rain
That did not stop until it ruined the riverbank

A flooded riverbank
A flooded, washed away riverbank
The waterlogged home of the toad

A toad
A thin toad
A thin, silent toad

Holly Patterson

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SUMMARY

Identifying the factors that promote co-existence of species has been a central debate in ecology for decades. The main controversy has been on the mechanisms controlling co-existence of species. Are species excluded from their potential ranges because of the abiotic environment or biotic interactions? In this context, habitat selection is an important process affecting the abundance and distribution of species; and differential habitat selection is considered as a mechanism that facilitates co-existence of species. Here, I studied the selection of aquatic (chapter 4) and terrestrial habitat (chapter 1-3) of pond-breeding amphibian species to shed more light on the mechanisms underlying the co-existence of species with complex life cycles. Moreover, I quantified the performance of aquatic anuran larvae to explore whether the selection of aquatic breeding habitat is a fitness-relevant process (chapter 5).

Chapter 1. Terrestrial space use and habitat selection are best studied by radio-tracking methods. Otherwise, repeated observations on cryptic animals are not possible. During tracking studies, the behavior of animals may be affected by the tracking and tagging methods used, which may influence the results obtained. We therefore evaluated the impact of transmitter mass and the duration of tracking period on body mass change of two anuran species that were fitted with externally attached radio transmitters. *Bufo b. spinosus* and *B. viridis* were radio-tracked for three months during summer in the active tract of a large gravel-bed river (Tagliamento River, NE Italy). Our results demonstrated that neither transmitter mass nor the duration of the tracking period affect body mass change of the two anurans in their terrestrial summer habitats. This implies that the movement data, which was used to study terrestrial habitat selection (chapters 2-3), was unlikely biased by the methods applied. Therefore, we encourage the use of externally attached radio-transmitters in amphibian ecology.

Chapter 2. We explored why animals restrict their behaviors to areas that are considerably smaller than expected from observed levels of mobility – so called home-ranges. We asked, which factors control the size of terrestrial summer home-ranges of anurans, and does the impact of factors vary with the home-range definition (spatial scale) used? Essentially, we quantified the effect of habitat, biotic and individual factors on individual home-range size of the European common toad (*Bufo b. spinosus*) and the Green toad (*Bufo viridis*) that were radio-tracked in their terrestrial summer habitat. Analyses were done for two spatial scales that differed in their intensity of use: small core areas within home-ranges with highest intensity of use, which is where animals spend 50% of their time, and large peripheral areas of home-ranges (95%-home-range excluding the 50% core area).

During the summer period amphibians need abundant food to build up fat reserves for maintenance and future reproduction, as well as thermal and predatory refuge. Hence, resting and foraging are the dominating behaviors in summer. And, these behaviors may segregate spatially because of non-overlapping distributions of food and shelter. Based on these assumptions we formulated three hypotheses that were expected to apply to both species: (H1) Habitat factors (habitat structure, home-range temperature) control the size of 50% core areas; (H2) biotic factors (prey density and competition) control the size of 95% home-ranges (excluding the 50% core area); and (H3) the effects of individual factors (body mass, sex, animal identity) on 50% core areas and 95% home-ranges are outweighed by habitat and biotic factors. The 50% core area of *B. b. spinosus* was best explained by habitat structure and prey density, whereas the 50% core area of *B. viridis* was determined solely by habitat structure. This suggests that the resting and foraging areas of *B. b. spinosus* are not spatially separated. The 95% home-range of *B. b. spinosus* was determined by prey density, while for *B. viridis* both habitat structure and prey density determined home range size.

We conclude that the terrestrial area requirements of amphibians depend on the productivity and spatiotemporal complexity of landscapes and that differential space use may facilitate their co-existence. The particular contribution of this study was our emphasis on behavior-based scale definitions. Behavior-based scale definitions facilitate the formulation of *a priori* hypotheses, thereby contributing to a better grounding of home-range studies in theory. Moreover, we showed how the interrelatedness of factors, which is typically inherent in field studies, can be handled. Finally, the usage of two sympatric species differing in ecology allowed shedding more light on the processes structuring home-ranges as well as the mechanisms that may facilitate co-existence in terrestrial habitats.

Chapter 3. In the previous chapter we determined the factors affecting the spatial dimension of home-ranges. Here, we asked, which factors determine the occurrence of species within large areas (floodplain) and within their home-ranges? Moreover, does the occurrence in terrestrial habitats vary across spatial scales? Specifically, we quantified the selection of terrestrial summer habitats in a complex floodplain by two sympatric amphibians (*Bufo b. spinosus* and *B. viridis*) as a function of habitat type, a biotic (prey density) and an abiotic resource (temperature). We applied a novel resource selection model, accounting for differences among individuals, at three spatial scales: a) home-range placement within the floodplain, b) space use within 95% home-ranges, and c) space use within 50% core areas.

We hypothesized that home-range placement is determined by both prey density and temperature because they are essential factors in summer for both species (H1). Summer home-ranges integrate spacious foraging and confined resting behavior. We therefore hypothesized that habitat use within 95% of home-ranges is determined by prey density (H2) and within 50% core areas by temperature (H3). Last, we predicted that the two species exhibit differential resource selection for shared habitat types across spatial scales (H4) because this would facilitate co-existence.

Habitat selection of both species across all spatial scales was best explained by a model including habitat type, prey density, temperature, and all interactions. Hence, H1 was fully supported whereas H2 and H3 were partially supported. This result suggests that amphibians perceive resource gradients at all spatial scales, and that all spatial scales are important for foraging behavior and thermoregulation.

Both species largely preferred the same habitat types. The same habitat types, however, were used differently in relation to resources across the three spatial scales, supporting hypothesis 4. Niche differentiation through differential resource selection within shared habitat types across spatial scales may therefore facilitate the co-existence of the two species in terrestrial summer habitats. Home-range placement was determined by the availability of habitat types rather than resources. Within both 95% home-ranges and 50% core areas, space use was strongly dependent on resources. To graphically explore the interactive effects of habitat type, prey density, and temperature we predicted habitat selection using the best selected model. We found that home-range placement did not depend on resource availability, which was puzzling as the terrestrial summer habitat should provide all essential resources for individual maintenance and survival. Moreover, animals placed home-ranges in floodplain areas where prey density was higher and temperature lower than outside home-ranges. It indicates that home-range placement can be influenced by intrinsic factors such as genetic differences between species, whereas space use within home-ranges is determined by resource gradients.

Chapter 4. We quantified breeding site selection of two pond-breeding toad (*Bufo bufo spinosus, B. viridis*) and two frog species (*Rana temporaria, R. latastei*) in relation to the separate and combined effects of landscape composition, hydrogeomorphology, abiotic and biotic conditions in ponds scattered patchily on a dynamic floodplain.

The rate of co-occurrence of *B. b. spinsous* with frogs was 17.3% and with *B. viridis* 12.4%, and all four species co-occurred in 1.5% of the sites. Co-occurrence rates were higher than expected based on neutral processes. "Neutral" means that species are identical in their ecology. Landscape composition, hydrogeomorphology, abiotic and biotic factors jointly affected breeding site selection. While breeding site selection was species-specific and guided by abiotic and biotic factors, it was not affected by the presence of other anuran species. Abiotic conditions and pond size affected pond selection of toads, but not frogs. Hence, our results do not support the role of competition avoidance in governing current breeding site selection. *Bufo b. spinosus* and *R. latastei* favored high predation risk ponds while *B. viridis* and *R. temporaria* avoided them. We provide evidence that differential habitat use and differences in response to abiotic factors and predation risk together may override competitive interactions, thereby facilitating local co-existence of species. Our main result is that "life attracts life", which indicates that characteristics of the favourable ponds covary among anurans and fish. Ponds that allow high local diversity of freshwater communities are large, deep, warm, and structurally complex.

Chapter 5. We quantified larval performance (body size at metamorphosis, growth rate, population density at metamorphosis) of a patchily distributed population of *B. b. spinosus* tadpoles in ponds of the active tract and of the riparian forest in an unconstrained alpine floodplain. Our main goals were i) to determine whether tadpole performance in the two main habitat types, the active tract and the riparian forest, is different, and ii) to quantify the impact of factors governing differences in larval performance between habitat types and among ponds in general. For the second question, our focus was on among-pond variation in body size at metamorphosis, an important life history trait for species with complex life cycles. The studied ponds differed with respect to hydroperiod, temperature, and predation risk. Warm ponds with more variable hydroperiod containing few predators were primarily located in the active tract, and ponds with opposite characteristics in the riparian forest.

Tadpoles from the active tract metamorphosed three weeks earlier and tended to be at a larger size than tadpoles from the riparian forest. In addition, population density at metamorphosis in the active tract was about one to two order of magnitudes larger than in the riparian forest. Larval mortality in the active tract was about 16% lower than in the riparian forest. These habitat type-specific differences in larval performance clearly show that the selection of breeding sites is a fitness-relevant process.

Spatial variation in body size at metamorphosis was governed by the direct and interactive effects of abiotic and biotic factors. Impacts of intraspecific competition on body size at metamorphosis were evident only at high temperature. Predation and intraspecific competition jointly reduced metamorphic size. At low intraspecific competition, predation limited growth while at high competition, predation increased growth.

The ponds in the active tract seem to be pivotal for the performance of anuran larvae and hence population persistence. The maintenance of this habitat type depends on a natural river bed and flow regime. River restorations seem therefore promising to increase the availability of high quality habitats that improve larval performance.

In conclusion, our results demonstrate that differential space use and differential resource selection within shared habitat types may facilitate co-existence of amphibians in terrestrial summer habitats. Similarly, differential habitat type preferences and ecological segregation along environmental gradients permit co-existence in the larval anuran community at the pond-level. Competitor avoidance currently appears to play a minor role in breeding site selection, thereby contrasting with classical expectations. The typically high variation in environmental conditions that are maintained by disturbances such as droughts and floods most probably outweighed competitive effects. In addition, habitat type-specific differences in larval performance clearly showed that the selection of aquatic breeding habitat is a fitness-relevant process. In summary, differential habitat selection is likely evident in all life history stages of amphibians, and most probably facilitates temporal co-existence of species with complex life cycles at local spatial scales.

Conservation implications. The present work has implications for the conservation of amphibians in both aquatic and terrestrial habitats. We found that niche-differentiation in both aquatic and terrestrial habitat was facilitated by large variation in environmental conditions. Hence, variation in environmental conditions is fundamental for niche-differentiation and high species diversity at the local scale. Disturbances such as droughts and floods maintain the high variation in environmental conditions observed. We therefore need to restore natural disturbance regimes to maintain environmental gradients and hence high local species diversity.

The habitat type large wood deposit was an important determinant of terrestrial home-range size, and preferred by both toad species studied. This habitat type provides thermal and predatory shelter. Reducing the availability of large wood by harvesting or flow regulation will most likely result in usage of less suitable thermal and predatory refuge. Consequently, mortality may increase and toad abundance decrease. The availability of large wood deposits within the active tract of the Tagliamento river depends on a fringing riparian forest and a dynamic flow regime. River restorations are therefore promising to provision and maintain the availability of large wood deposits as well as to create the structural habitat diversity that is required for various behaviors in terrestrial habitats.

Larval performance was best in ponds of the active tract, emphasizing their role for population persistence. Large, shallow, warm, and low predation risk ponds in the active tract led to improved larval performance. The creation and

maintenance of ponds in early succession stages depends on a natural river bed and flow regime and an unconstrained river morphology as well. Again, river restorations are a promising method to create and maintain habitats of early succession stages that are favorable for tadpole performance. This does not mean that ponds of old succession stage in the riparian forest are not important for larval productivity. In contrary, ponds in the riparian forest are better protected from floods and may contribute, though marginally, to population growth even in the case of floods. In the active tract, floods may result in catastrophic mortality. Hence, all pond-types contribute to population growth and are most probably important for population persistence. The perimeter for future river restorations should therefore include the fringing riparian forest as well.

ZUSAMMENFASSUNG

Die Identifikation von Faktoren, welche Koexistenz von Arten ermöglichen ist seit Jahrzehnten ein zentrales und kontrovers diskutiertes Thema der Ökologie. Die Diskussion dreht sich vor allem um die Mechanismen welche Koexistenz ermöglichen. Limitieren abiotische Faktoren oder biotische Interaktionen die Verbreitung von Arten? In diesem Zusammenhang ist Habitatselektion ein wichtiger Prozess, der die Abundanz und Verbreitung von Arten beeinflusst; und differenzielle Habitatselektion ist einer der Mechanismen, welcher Koexistenz ermöglicht. Um Koexistenz von Arten mit komplexen Lebenszyklen besser zu verstehen, quantifizierte ich im Rahmen dieser Dissertation Habitatselektion von semi-aquatischen Amphibien sowohl im aquatischen (Kapitel 4) als auch im terrestrischen Habitat (Kapitel 1-3). Zudem quantifizierte ich die Fitness-Konsequenzen aquatischer Habitatselektion (Kapitel 5).

Kapitel 1. Radiotelemetrische Methoden sind bestens geeignet, um Raumverhalten von Tieren zu studieren. Keine andere Methode ermöglicht kontinuierliches Beobachten versteckt lebender Tiere wie bspw. von Amphibien. Markierungsmethoden, und dazu gehören radiotelemetrische Methoden, können das natürliche Verhalten von Tieren beeinflussen, und damit Resultate verfälschen. Wir quantifizierten den Einfluss von Transmittergewicht und Besenderungsdauer auf Gewichtsveränderungen zweier Krötenarten (Kapitel 1). Transmitter wurden extern mit einem Hüftgurt am Tier befestigt. Zahlreiche Individuen der Erdkröte (*Bufo b. spinosus*) und der Wechselkröte (*B. viridis*) wurden während der Sommerperiode (Juli-September) im aktiven Geschiebebereich des Tagliamentoflusses in Norditalien telemetriert. Unsere Resultate belegen, dass weder das Transmittergewicht noch die Besenderungsdauer Gewichtsveränderungen beider Krötenarten beeinflussen. Dies impliziert, dass das natürliche Verhalten der Kröten nicht beeinflusst war, und somit die Raumnutzungsdaten welche wir zur Quantifikation von terrestrischer Habitatselektion verwendet haben nicht von Methodeneffekten überlagert sind (Kapitel 2-3). Aufgrund vorliegender Resultate empfehlen wir den Einsatz extern befestigter Transmitter in der Amphibienökologie.

Kapitel 2. Weshalb Tiere Ihre Aktivitäten/Verhalten auf Flächen beschränken die weitaus kleiner sind als man aufgrund der beobachteten Mobilität erwarten kann, so genannte home-ranges, hat bereits Darwin beschäftigt. Ortstreue beeinflusst die Verbreitung von Arten, und die Mechanismen welche Ortstreue bewirken werden bis heute kontrovers diskutiert. Wir fragten deshalb: "Welche Faktoren regulieren die Grösse des terrestrischen Sommerlebensraumes (Sommer-home-range) von Amphibien? Und, variiert der Einfluss der Faktoren mit der räumlichen Skala?" Wir quantifizierten den Einfluss von Habitatfaktoren, von biotischen und individuellen Faktoren auf die Grösse des Sommerlebensraumes zweier Krötenarten. Während des Sommers telemetrierten wir Erdkröten und Wechselkröten in aktiven Geschiebebereich des Tagliamento, einem frei fliessenden, morphologisch und hydrologisch intakten Alpenfluss. Alle Analysen wurden für zwei räumliche Skalen durchgeführt. Diese räumlichen Skalen unterschieden sich in ihrer Nutzungsintensität: so genannte 50% core areas mit höchster Nutzungdichte und 95% home-ranges (ohne 50% core area) mit geringerer Nutzungsdichte. Die 50% core area ist relative klein, liegt innerhalb des home-ranges und umfasst 50% der Peilungen. Das heisst, das Tier hat in der 50% core area die Hälfte seiner Zeit verbracht. Der 95% home-range umfasst die 50% core area und grosse periphere Flächen ausserhalb der core area.

Während des Sommers benötigen Amphibien ausreichend Beute, um sich Fettreserven für die Reproduktion im nächsten Frühjahr anzulegen, und Unterschlupf der vor Fressfeinden und Austrocknung schützt. Beute- und Unterschlupfdichte sind demnach die wichtigsten Faktoren während der Sommerperiode welche Ruhe- und Jagdverhalten regulieren. Ruhe- und

Jagdverhalten können räumlich separiert sein, wenn Beute und Unterschlupf unterschiedlich verteilt sind. Aufgrund dieser Annahmen formulierten wir drei Hypothesen, welche für beide Krötenarten gelten: (H1) Habitatfaktoren (Habitat struktur als Surrogat für Unterschlupfdichte, ausgedrückt durch Habitatdiversität und Schwemmholzfläche; home-range Temperatur) regulieren die Grösse der 50% core area; (H2) biotische Faktoren (Beutedichte, Konkurrenz) regulieren die Grösse der 95% home-ranges (exklusive der 50% core area); und (H3) Einflüsse individueller Faktoren (Körpermasse, Geschlecht, Tieridentität=Tiernummer) auf die 50% core area und den 95% home-range werden von Habitatfaktoren und biotischen Faktoren überlagert.

Die Grösse der 50% core area der Erdkröte wurde am besten durch Habitatstruktur und Beutedichte erklärt. Die 50% core area der Wechselkröte wurde nur durch Habitatstruktur erklärt. Diese Resultate implizieren, dass Ruhe- und Jagdverhalten der Erdkröte räumlich nicht getrennt sind. Die Grösse des 95% home-ranges der Erdkröte wurde nur durch die Beutedichte bestimmt. Die Grösse des 95% home-ranges der Wechselkröte hingegen wurde zu gleichen Anteilen durch Habitatstruktur und Beutedichte reguliert.

Unsere Resultate zeigen, dass die terrestrischen Habitatansprüche von Amphibien von der Produktivität und räumlichen Komplexität des Lebensraumes abhängen. Differenzielle Habitatnutzung kann die Koexistenz der gemeinsam verbreiteten Krötenarten im terrestrischen Sommerlebensraum ermöglichen. Die Innovation dieser Studie liegt in der Verknüpfung von Verhalten mit der räumlichen Skala. Dies ermöglicht die Formulierung von *a priori* Hypothesen, und trägt somit zur besseren Einbettung von home-range Studien in ökologischer Theorie bei. Zudem quantifizierten wir die direkten und indirekten Effekte von Faktoren auf die Lebensraumgrösse, und zeigen damit auf wie mit typischerweise korrelierten Faktoren aus Feldstudien umgegangen werden kann.

Kapitel 3. Im letzten Kapitel bestimmten wir die Faktoren welche die Grösse des terrestrischen Sommerlebensraumes regulieren. Hier fragen wir:

“Welche Faktoren bestimmen, wo sich ein Tier innerhalb des Studiengebietes und des home-ranges aufhält?“ Wir quantifizierten dazu Habitatselektion von Erd- und Wechselkröten im terrestrischen Sommerlebensraum. Habitatselektion quantifizierten wird als Funktion von Habitattyp, einer biotischen (Beutedichte) und einer abiotischen Ressource (Temperatur). Drei räumliche Skalen wurden verwendet: a) Home-range-Selektion innerhalb des Studiengebietes (aktiver Geschiebebereich des Tagliamento), b) Habitatnutzung innerhalb 95% home-ranges, und c) Habitatnutzung innerhalb 50% core areas.

Wir erwarteten, dass home-range-Selektion innerhalb des Studiengebietes durch alle Faktoren beeinflusst wird, welche während der Sommerperiode wichtig sind: Beutedichte und Temperature (H1). Ruhe- und Jagdverhalten dominieren während des Sommers. Ruheverhalten kann auf kleinstem Raum stattfinden, für Jagdverhalten werden grössere Flächen beansprucht. Wir erwarteten deshalb, dass Habitatnutzung innerhalb der grossen 95% home-ranges durch Beutedichte (H2) und innerhalb der 50% core areas durch Temperatur (H3) reguliert wird. Zudem erwarteten wir, dass beide Arten Ressourcen innerhalb derselben Habitattypen unterschiedlich nutzen (differentielle Habitatnutzung) (H4), weil dies Koexistenz im terrestrischen Sommerlebensraum ermöglichen würde.

Habitatselektion beider Arten variierte in Abhängigkeit der räumlichen Skala. Das komplexeste Modell, welches die additiven und interaktiven Effekte von Habitattyp, Beutedichte und Temperatur beinhaltete, erklärte Habitatselektion beider Arten auf jeder räumlichen Skala am besten. Unsere Resultate unterstützen deshalb H1 vollständig, die Hypothesen H2 und H3 jedoch nur teilweise. Unsere Resultate implizieren, dass beide Ressourcen für die Regulation von Ruhe- und Jagdverhalten wichtig sind, unabhängig von der räumlichen Skala. Zudem scheinen Amphibien in der Lage zu sein, die Verfügbarkeit von Ressourcen innerhalb des Studiengebietes und innerhalb ihrer home-ranges abschätzen zu können.

Beide Arten bevorzugten im Grossen und Ganzen die gleichen Habitattypen. Dieselben Habitattypen wurden jedoch auf jeder der drei räumlichen Skalen unterschiedlich in Bezug auf die Ressourcen Bedeutedichte und Temperatur genutzt, was unsere Erwartung bestätigte (H4). Nischendifferenzierung durch differenzielle Ressourcennutzung innerhalb gleich bevorzugter Habitattypen kann deshalb Koexistenz im Sommerlebensraum ermöglichen, auf jeder räumlichen Skala. Wir verwendeten das beste und hier gleich auch komplexeste Modell zur Vorhersage von Habitatselektion, um die interaktiven Effekte von Habitattyp, Beutedichte, und Temperatur auf die Habitatselektion grafisch darzustellen. Unsere Vorhersagen zeigten, dass home-range-Selektion im Studiengebiet mehr vom Angebot der Habitattypen als vom Angebot der Ressourcen bestimmt wird. Dieses Resultat erstaunte, weil wir zeigten, dass die Beutedichte innerhalb der 95% home-ranges grösser war als ausserhalb der home-ranges. Auch die Temperatur war innerhalb der 95% home-ranges tiefer als ausserhalb; und tiefe Temperaturen verringern die Austrocknungsgefahr. Habitatnutzung innerhalb der 95% home-ranges und 50% core areas hingegen wurde durch die Verfügbarkeit von Ressourcen bestimmt. Diese Resultate zeigen, dass home-range-Selektion innerhalb grosser Gebiete (hier Studiengebiet) zusätzlich durch intrinsische Faktoren (genetische Unterschiede, Unterschiede in der Erfahrung/Alter) beeinflusst wird. Habitatnutzung innerhalb der home-ranges hingegen wird vorwiegend durch Ressourcen-Gradienten reguliert.

Kapitel 4. Wir quantifizierten die Laichgewässern-Selektion zweier Krötenarten (*Bufo bufo spinosus, B. viridis*) und zweier Froscharten (*Rana temporaria, R. latastei*), in Abhängigkeit der separaten und interaktiven Effekte von Habitattyp, hydrogeomorphologischen Faktoren, abiotischen und biotischen Konditionen. Die Laichgewässer waren unregelmässig im aktiven Geschiebebereich und dem angrenzenden Auenwald des Tagliamentoflusses verteilt.

B. b. spinosus kam gemeinsam mit Fröschen in 17.3% und mit *B. viridis* in 12.4% der Laichgewässer vor. Alle Arten kamen gemeinsam in 1.5% der Laichgewässer vor. Diese Prozentzahlen sind höher, als aufgrund "neutraler Prozesse" zu erwarten wäre. „Neutral" bedeutet, dass die Arten bezüglich ökologischer Ansprüche identisch sind. Die Selektion der Laichgewässer wurde durch die additiven und interaktiven Effekte von Habitattyp, hydrogeomorphologischen Faktoren, abiotischen- und biotischen Konditionen bestimmt. Zudem erfolgte Laichgewässer-Selektion artspezifisch, d.h. alle Arten zeigten unterschiedliche Präferenzen für abiotische und biotische Faktoren. Bereits besetzte Laichgewässer wurden nicht gemieden, sondern klar bevorzugt. Der vorherrschende Einfluss von Konkurrenz auf die Laichgewässer-Selektion, und somit Verbreitung von Arten, wird durch unsere Resultate nicht belegt. *B. b. spinosus* and *R. latastei* waren am häufigsten in Laichgewässern mit hohem Prädationsrisiko. *B. viridis* and *R. temporaria* mieden Laichgewässer mit hohem Prädationsrisiko. Unsere Resultate belegen, dass unterschiedliche Nutzung gleicher Habitattypen und unterschiedliche Reaktionen auf abiotische Konditionen sowie Prädationsrisiko Konkurrenz aushebeln können. Dadurch wird lokale Koexistenz ermöglicht. Unser Hauptresultat ist, dass "Leben Leben anzieht". Anders ausgedrückt, sowohl für Amphibien als auch für Fische sind dieselben Tümpelcharakteristika wichtig. Tümpel, welche artenreiche Tümpelgemeinschaften, sprich hohe lokale Diversität ermöglichen, sind gross, tief, warm und strukturreich.

Kapitel 5. In Kapitel 4 quantifizierten wird die Selektion aquatischer Habitate (Laichgewässer). Hier evaluierten wir, welche Konsequenzen die Laichgewässer-Selektion für das Wachstum der Larven (Kaulquappen) sowie deren Körpergrösse und Populationsdichte zum Zeitpunkt der Metamorphose hat. Wachstumsrate, Körpergrösse und Populationsdichte werden als so genannte Fitness-Komponenten oder „performance measures" bezeichnet. Wir quantifizierten diese Fitness-Komponenten für die Erdkröte. Larven der Erdkröte waren unregelmässig in Laichgewässern des aktiven Geschiebebereichs und des angrenzenden Auenwaldes des Tagliamentoflusses verteilt. Unsere Hauptziele waren: i) Fitness-Komponenten (Wachstumsrate, Körpergrösse und Populationsdichte bei Metamorphose) für die beiden wichtigsten Habitattypen zu quantifizieren: den aktiven Geschiebebereich und den Auenwald; ii) die Faktoren zu quantifizieren, welche die Körpergrösse bei Metamorphose regulieren. Körpergrösse bei Metamorphose ist ein wichtiges Merkmal. Es wird erwartet, dass grosse Metamorphlinge später im terrestrischen Lebensraum besser überleben, früher reproduzieren, und mehr Nachkommen produzieren als kleine Metamorphlinge. Die ausgewählten Tümpel unterschieden sich in Bezug auf die Länge der Hydroperiode (Dauer der Wasserführung), Temperatur und Prädationsrisiko. Warme Tümpel mit geringem Prädationsrisiko und variablerer Hydroperiode waren vorwiegend im aktiven Geschiebebereich verteilt. Tümpel mit gegenläufigen Charakteristika waren vorwiegend im Auenwald verteilt.

Larven im aktiven Geschiebebereich waren bei Metamorphose tendenziell grösser, und beendeten die Metamorphose drei Wochen früher ab als Larven im Auenwald. Zudem war die Populationsdichte bei Metamorphose im aktiven Geschiebebereich um ein bis zwei Grössenordnungen höher als im Auenwald. Die Mortalität der Larven war im aktiven Geschiebebereich um 16% tiefer als im Auenwald. Diese Resultate belegen, dass sich Fitness-Komponenten deutlich zwischen Habitattypen unterscheiden. Aquatische Habitatselektion ist deshalb ein fitnessrelevanter Prozess.

Räumliche Variation in der Körpergrösse bei Metamorphose wurde durch die direkten und interaktiven Effekte abiotischer und biotischer Faktoren bestimmt. Einflüsse intraspezifischer Konkurrenz auf die Körpergrösse bei Metamorphose wurden nur bei hohen Temperaturen erkennbar. Körpergrösse bei Metamorphose war negativ mit den interaktiven Effekten von Prädation und intraspezifischer Konkurrenz korreliert. Bei tiefer intraspezifischer Konkurrenz limitierte

Prädation das Wachstum. Bei hoher Konkurrenz hingegen steigerte Prädation das Wachstum.

Zusammengefasst zeigen unsere Resultate, dass Koexistenz im terrestrischen Sommerlebensraum durch unterschiedliche Raumnutzung und unterschiedliche Ressourcen-Nutzung innerhalb gleich bevorzugter Habitattypen ermöglicht wird. Koexistenz in aquatischen Habitaten wird durch ähnliche Mechanismen ermöglicht, durch Nischendifferenzierung entlang abiotischer und biotischer Gradienten. Konkurrenz scheint die Laichgewässer-Selektion nicht zu beeinflussen. Die ausgeprägte Variation von Umweltbedingungen, welche für dynamische Lebensräume typisch ist, hat Konkurrenzeffekte sehr wahrscheinlich überlagert. Diese grosse Variation von Umweltbedingungen wird durch Hochwasser und Trockenheiten aufrechterhalten; und diese Variation ermöglicht schliesslich hohe lokale Artendiversität. Unsere Resultate belegen zudem, dass aquatische Habitatselektion ein Prozess ist, der Fitness-Komponenten wesentlich beeinflusst. Differentielle Habitatselektion kommt vermutlich in allen Lebensstadien von Amphibien vor, und ermöglicht zeitliche und räumlich lokale Koexistenz von Arten mit komplexen Lebenszyklen.

Praxisrelevanz. Einige Resultate vorliegender These sind naturschutz-relevant. Ein Hauptergebnis war, dass Nischendifferenzierung im aquatischen und terrestrischen Habitat durch grosse Variation in Umweltbedingungen ermöglicht wird. Variation von Umweltbedingungen ist deshalb eine fundamentale Voraussetzung, um lokal hohe Artendiversität zu ermöglichen. Natürliche Störungen wie Trockenheiten und Hochwasser erhalten hohe Variation in Umweltbedingungen. Die Wiederherstellung einer natürlichen Abflussdynamik ist deshalb essentiell, um Umweltgradienten und deshalb lokal hohe Artendiversität zu erhalten.

Der Habitattyp „Schwemmholz" bestimmte die Grösse des terrestrischen Sommerlebensraumes der Wechselkröte wesentlich. Dieser Habitattyp bietet Schutz vor Austrocknung und Prädation im offenen Schotterbereich, welcher von der Wechselkröte dominiert wird. Eine Verringerung des Schwemmholz-Angebotes durch menschliche Nutzung oder Regulierung des Abflussregimes wird deshalb dazu führen, dass die Wechselkröte suboptimale Habiattypen zum Schutz vor Austrocknung und Prädation aufsucht. In der Folge dürfte Mortalität zunehmen und Abundanz abnehmen. Das Schwemmholz-Angebot im aktiven Geschiebebereich des Tagliamento wird vom angrenzenden Auenwald gespiesen. Wesentlich für den Schwemmholztransport und Eintrag sind gelegentliche Hochwasser. Flussrevitalisierungen scheinen deshalb geeignet, um das Schwemmholz-Angebot zu erhalten. Für die Wechselkröte bietet Schwemmholz die notwendige strukturelle Vielfalt, welche Thermoregulation und Schutz vor Prädation ermöglicht.

Wachstumsbedingungen für Amphibienlarven waren am besten in grossen, flachen, und warmen Tümpeln des aktiven Geschiebebereichs mit geringem Prädationsrisiko. Diese Tümel werden regelmässig überflutet und trocknen gelegentlich aus. Dadurch wird deren Sukzession verlangsamt, und Prädatoren vermögen sich nicht in hoher Dichte zu etablieren. Die Erhaltung junger Laichgewässer hängt von einem natürlichen Flussbett und einem natürlichen Abflussregime ab. Wiederum, Flussrevitalisierungen scheinen geeignet, um die Erhaltung junger Laichgewässer zu gewährleisten, die gute Wachstumbedingungen für Amphibienlarven bieten. Das bedeutet nicht, dass Waldtümpel (späte Sukzessionsstadien), keine Relevanz für das Populationswachstum haben. Im Gegenteil, Waldtümpel sind besser vor Hochwasser geschützt und könnten deshalb in Jahren mit Hochwassern zum Populationswachstum beitragen. Das heisst, die Produktivität von Waldtümpeln ist klein, aber über längere Zeiträume gesehen relativ konstant. Tümpel im aktiven Geschiebebereich hingegen tragen nur in Jahren ohne Hochwasser zum

Populationswachstum bei. Für die Persistenz von Amphibienpopulationen scheint deshalb die Erhaltung unterschiedlicher Laichgewässertypen wichtig. Bei Flussrevitalisierungen sollte der Perimeter deshalb auch den angrenzenden Auenwald umfassen.

RIASSUNTO

Da decenni gli ecologi si interrogano sui parametri che determinano la coabitazione di specie diverse. La maggiore controversia concerne i meccanismi che stabiliscono la coabitazione: l'assenza di alcune specie da un ambiente potenzialmente favorevole è dovuta a fattori abiotici o a interazioni biotiche? La selezione dell'habitat è un processo importante che influenza l'abbondanza e la distribuzione delle specie e la scelta di nicchie differenziate è uno dei meccanismi che facilitano la coabitazione. In questo contesto abbiamo studiato la selezione dell'habitat acquatico (capitolo 4) e terrestre (capitoli 1-3) da parte di anfibi che depongono le uova in stagni, allo scopo di far luce sui meccanismi che determinano la coabitazione di specie dal ciclo vitale complesso. Abbiamo inoltre misurato le caratteristiche fisiche delle larve di anuri acquatici, allo scopo di definire se l'habitat acquatico in cui si sviluppano influenza la loro prestazione fisica (capitolo 5).

Capitolo 1. L'impiego di radio-trasmettitori permette di studiare al meglio la gestione dello spazio e la selezione dell'habitat da parte di animali dal mimetismo criptico, che non sarebbe possibile osservare altrimenti su un lungo periodo. Durante gli studi con i radio-trasmettitori il comportamento degli animali può essere influenzato dal metodo di trasmissione impiegato, modificando i risultati. Abbiamo quindi valutato l'impatto della massa del trasmettitore e della durata della ricerca sulla massa corporea di due anuri sui cui sono stati fissati radio-trasmettitori esterni (capitolo 1). *Bufo b. spinosus* e *B. viridis* sono stati studiati per tre mesi, durante l'estate, in un ramo secondario del fiume Tagliamento, un corso d'acqua largo e dal fondo ghiaioso del nord-est Italia, morfologicamente e idrologicamente intatto. I risultati ottenuti dimostrano che né la massa del trasmettitore, né la durata della ricerca, influenzano la massa corporea dei due anuri nel loro habitat terrestre estivo. I dati relativi ai movimenti delle due specie di rospi, utilizzati per studiare la selezione dell'habitat terrestre (capitoli 2-3), non sembrano quindi subire l'influenza del metodo utilizzato. Per questo motivo raccomandiamo l'uso di radio-trasmettitori per studiare l'ecologia degli anfibi.

Capitolo 2. Abbiamo cercato di capire perché gli animali si muovono soprattutto entro un territorio decisamente inferiore al loro potenziale di mobilità –il cosiddetto *home-range*. Ci siamo chiesti quali fattori determinano la dimensione dell'*home-range* estivo terrestre degli anuri e se l'impatto di tali fattori varia a seconda della definizione di "*home-range*" che si utilizza (scala territoriale). Abbiamo misurato l'effetto sia del contesto biotico, sia di fattori individuali, sulla dimensione dell'*home-range* del rospo comune europeo (*Bufo b. spinosus*) e del rospo smeraldino (*Bufo viridis*); entrambi sono stati seguiti nei loro spostamenti all'interno del loro habitat terrestre estivo, grazie a radio-trasmettitori. Due scale territoriali, diverse per intensità d'uso, sono state analizzate: da un lato una zona centrale più piccola, ove si osserva la più elevata intensità d'uso, ossia dove gli animali trascorrono il 50% del proprio tempo; dall'altro un'area più ampia, che comprende le zone periferiche dell'*home-range*, dove gli animali trascorrono il 95% del resto del tempo (ossia il 95% del tempo che trascorrono al di fuori dell'area centrale dove invece stazionano per il 50% del tempo).

Durante l'estate gli anfibi necessitano di cibo in abbondanza per fabbricare le riserve di grasso necessarie alla riproduzione, come pure di un rifugio che li protegga dalle aggressioni climatiche e dai predatori. Per questo motivo riposare e cacciare sono le principali attività estive. Queste due attività possono avvenire in luoghi diversi poiché nutrimento e rifugio spesso non si trovano nello stesso luogo all'interno dell'*home-range*. Sulla base di questo presupposto abbiamo formulato tre ipotesi, valide per entrambe le specie: (H1) Il tipo di habitat (struttura dell'habitat, temperatura nell'*home-range*) determinano la dimensione della zona centrale ("zona-50%"); (H2) fattori biotici (densità di prede e concorrenza) determinano invece la dimensione dell'area più ampia ("zona-

95%”); e (H3) fattori individuali (quali massa corporea, sesso, singolarità dell’animale) influenzano in modo irrilevante la dimensione della zona-50% e della zona-95%, rispetto al tipo di habitat e ai fattori biotici che sono invece fattori determinanti. La zona-50% per *B. b. spinosus* è determinata soprattutto dalla struttura dell’habitat e dalla densità di prede, mentre per *B. viridis* essa è determinata unicamente dalla struttura dell’habitat. Se ne deduce che le zone di riposo e di caccia di *B. b. spinosus* non sono separate. La zona-95% di *B. b. spinosus* è determinata dalla densità di prede, mentre per *B. viridis* essa è determinata sia dalla struttura dell’habitat, sia dalla densità di prede.

Se ne deduce quindi che l’*home-range* terrestre degli anfibi dipende dalla produttività e dalla complessità spazio-temporale del paesaggio e che un uso differenziato dello spazio può facilitare la coabitazione di specie diverse. Questo studio ha evidenziato il ruolo del comportamento animale nella definizione della dimensione del proprio *home-range*. Studiare il legame tra la dimensione di un territorio animale e il comportamento dell’animale stesso facilita la formulazione di ipotesi *a priori* e in questo modo contribuisce a consolidare le fondamenta degli studi sul comportamento territoriale. Questa ricerca ha inoltre mostrato come è possibile gestire l’analisi di fattori intercorrelati, come si trovano spesso in natura. Infine, la scelta di due specie simpatriche, ma ecologicamente diverse, ha permesso di chiarire ulteriormente il processo di definizione dell’*home-range* come pure il meccanismo che facilita la coabitazione negli habitat terrestri.

Capitolo 3. Nei capitoli precedenti abbiamo determinato quali fattori influenzano la dimensione dell’*home-range*. In questo capitolo abbiamo studiato invece i fattori che determinano dove si trova l’animale all’interno dell’*home-range*. Inoltre ci siamo chiesti se il luogo in cui si trova un animale all’interno dell’habitat terrestre cambia modificando la scala territoriale. In particolare abbiamo studiato la scelta dell’habitat terrestre estivo in una complessa zona di caccia di due anfibi simpatrici (*Bufo b. spinosus* e *B. viridis*) in funzione del tipo di habitat, delle risorse biotiche (densità di prede) e di quelle abiotiche (temperatura). Abbiamo applicato un nuovo modello di selezione delle risorse che tenga conto delle differenze individuali, a tre livelli di scala territoriale: a) *home-ranges* all'interno della zona di caccia, b) utilizzazione dello spazio all'interno della zona-95%, e c) utilizzazione dello spazio all'interno della zona-50% centrale.

Abbiamo ipotizzato che lo stazionamento nell'*home-range* è determinato sia dalla densità di prede, sia dalla temperatura, perché entrambi i fattori sono fondamentali in estate per entrambe le specie (H1). I territori estivi comprendono ampie zone di caccia e zone di riposo più ridotte. Per questo motivo abbiamo ipotizzato che l'uso dell'habitat all'interno della zona-95% dell'*home-range* è determinato dalla densità di prede (H2) mentre all'interno della zona-50% (centrale) è determinato dalla temperatura (H3). Abbiamo infine supposto che le due specie selezionano le risorse in modo diverso all'interno dello stesso *home-range,* a diversi livelli di scala territoriale (H4), perché questo facilita la coabitazione.

La selezione dell'habitat da parte delle due specie a tutti i livelli di scala territoriale è risultata coincidere con un modello comprendente il tipo di habitat, la densità di prede, la temperatura, e tutte le interazioni. In questo modo, H1 è risultata essere interamente confermata mentre H2 e H3 sono apparse giustificate solo parzialmente. Questo risultato suggerisce che gli anfibi percepiscono gradienti di risorse a tutti i livelli di scala territoriale, e che tutti i livelli di scala territoriale sono importanti per determinare il comportamento predatorio e la termoregolazione.

Le due specie hanno mostrato di prediligere in gran parte gli stessi tipi di habitat. Gli stessi tipi di habitat, tuttavia, sono stati usati in modo diverso dalle due specie, dal punto di vista delle risorse, nei tre livelli di scala territoriale, sostenendo l'ipotesi 4. La coabitazione delle due specie all'interno di uno stesso tipo di habitat terrestre estivo è facilitata dall'occupazione di nicchie ecologiche diverse a causa di una diversa selezione delle risorse, nei vari livelli di scala territoriale. La delimitazione dell'*home-range* è stata determinata dal tipo di habitat disponibile piuttosto che dalle risorse. All'interno di entrambe le zone (la zona-95% e la zona-50%) invece, l'utilizzazione dello spazio è risultata essere nettamente legata alle risorse disponibili. Per studiare graficamente gli effetti interattivi del tipo di habitat, della densità di prede e della temperatura, abbiamo ipotizzato una selezione dell'habitat utilizzando il miglior modello disponibile. Sorprendentemente abbiamo osservato che la delimitazione dell'*home-range* non dipende dalla disponibilità delle risorse, sebbene l'habitat estivo terrestre debba fornire tutte le risorse fondamentali per la conservazione e la sopravvivenza degli individui. D'altro canto, gli animali hanno situato il proprio *home-range* in zone di caccia in cui la densità di prede era superiore e la temperatura inferiore rispetto all'esterno. In conclusione questo risultati dimostrano che la delimitazione dell'*home-range* può essere influenzata da fattori intrinseci come p. es. differenze genetiche tra le specie, mentre l'utilizzazione dello spazio all'interno dell'*home-range* è determinata dai gradienti di risorse disponibili.

Capitolo 4. Abbiamo studiato la scelta del sito per la riproduzione da parte di due rospi che depongono le uova in stagni (*Bufo bufo spinosus, B. viridis*) e di due rane (*Rana temporaria, R. latastei*) mettendola in relazione con gli effetti separati e combinati della configurazione dell'habitat, dell'idrogeomorfologia, e delle condizioni biotiche e abiotiche in stagni distribuiti in modo irregolare in un ramo secondario del fiume Tagliamento e nell'adiacente bosco golenale.

Abbiamo osservato una percentuale di coabitazione (sovrapposizione dell'*home-range*) di *B. b. spinosus* con le rane del 17.3% e con *B. viridis* del 12.4%, mentre abbiamo osservato una coabitazione di tutte e quattro le specie nell'1.5% dei siti. Abbiamo osservato una percentuale di coabitazione superiore a quanto ipotizzabile in una "situazione neutra". Con "situazione neutra" si intende una situazione in cui le specie sono identiche dal punto di vista ecologico. La configurazione dell'habitat, l'idrogeomorfologia, e i fattori biotici e abiotici insieme determinano la scelta del sito per la riproduzione. Essa è specifica per ogni specie ed è determinata da fattori abiotici e biotici, ma non è influenzata dalla presenza o meno di altre specie di anuri. La scelta dello stagno per la riproduzione da parte dei rospi è determinata da condizioni abiotiche e dalle dimensioni dello stagno, mentre non è così per le rane. *B. b. spinosus* e *R. latastei* hanno selezionato stagni a rischio di predazione da parte dei pesci, mentre *B. viridis e R. temporaria* li hanno piuttosto evitati. In altre parole, i risultati di questo studio non sostengono la tesi secondo cui la scelta del sito per la riproduzione sarebbe determinata dal desiderio di evitare la concorrenza. Questo studio mostra che un uso differenziato dell'habitat e reazioni diverse di fronte a fattori abiotici e al rischio predatorio possono annullare le interazioni concorrenziali, facilitando così la coabitazione di specie diverse. Il risultato principale, in questo senso, è l'osservazione che "la vita attira la vita", in altre parole le caratteristiche che rendono interessante uno stagno sono le stesse sia per gli anuri che per i pesci. Gli stagni che presentano un'alta diversità di specie d'acqua fresca sono ampi, profondi, caldi, e molto strutturati.

Capitolo 5. Abbiamo misurato la *performance* (dimensioni del corpo al momento della metamorfosi, tasso di crescita e densità della popolazione al momento della metamorfosi) dei girini di *B. b. spinosus,* distribuiti in modo irregolare nelle acque stagnanti di un ramo secondario del fiume e del bosco golenale adiacente, in un ambiente alpino naturale. Ci siamo posti i seguenti obiettivi i) determinare se la *performance* dei girini nei due principali tipi di habitat, il fiume e il bosco golenale, è diversa oppure no, e ii) determinare l'influenza dei vari fattori responsabili delle diverse *performance* dei girini, da un tipo di habitat all'altro e, in generale, da uno stagno all'altro. Per quanto riguarda la seconda domanda, ci siamo concentrati sulla differenza di dimensione del corpo dei girini da uno stagno all'altro, al momento della metamorfosi. Tale misura è un elemento chiave nello sviluppo delle specie con un ciclo vitale complesso. Gli stagni analizzati differivano in termini di regime idrico, temperatura, e rischio predatorio. Nel ramo secondario del fiume Tagliamento abbiamo osservato stagni più caldi, con periodi idrici più variabili e con meno predatori, mentre nel bosco golenale abbiamo osservato soprattutto stagni con caratteristiche opposte a quelle elencate.

La metamorfosi dei girini del ramo secondario di fiume è avvenuta tre settimane prima rispetto a quella dei girini del bosco golenale e con una dimensione corporea maggiore. Inoltre la densità della popolazione al momento della metamorfosi è risultata essere una o due volte maggiore nelle acque stagnanti del fiume rispetto a quelle del bosco golenale. Abbiamo osservato un tasso di mortalità dei girini nel fiume del 16% inferiore rispetto a quello dei girini del bosco golenale. Queste differenze di *performance,* legate al tipo di habitat, mostrano chiaramente che la scelta del sito per la deposizione delle uova influenza notevolmente la prestazione fisica e quindi la probabilità di sopravvivenza della prole.

Le differenze in termini di dimensioni corporee, al momento della metamorfosi, sono state dettate da fattori biotici e abiotici che hanno influito in modo diretto e interattivo. L'impatto della concorrenza intra-specie sulla dimensione corporea al momento della metamorfosi è apparso evidente unicamente a temperature elevate. L'effetto congiunto dei predatori e della concorrenza intra-specie causa una riduzione della dimensione corporea al momento della metamorfosi. In casi in cui la concorrenza intra-specie era bassa, la presenza di predatori ha limitato la crescita dei girini, mente in casi di elevata concorrenza la presenza di predatori ha causato un aumento della dimensione corporea.

Le acque stagnanti del ramo secondario del fiume sembrano essere di fondamentale importanza per la *performance* delle larve di anuri e quindi per la continuità della popolazione. La conservazione di questo tipo di habitat dipende dalla presenza di un corso d'acqua naturale e dal tipo di regime idrico. La rinaturazione dei corsi d'acqua appare dunque promettente dal punto di vista della disponibilità di habitat di alta qualità, favorevoli allo sviluppo dei girini.

In conclusione, questo studio ha dimostrato che l'uso differenziato dello spazio e una diversa selezione delle risorse all'interno di uno stesso habitat possono facilitare la coabitazione di anfibi in un habitat terrestre estivo. Analogamente, il fatto di operare scelte diverse in termini di habitat e la segregazione ecologica entro gradienti ambientali, permettono la coabitazione di girini di anuri in uno stesso stagno. Evitare la concorrenza non sembra essere un criterio di rilievo nella scelta del sito per la riproduzione, e questo in contrasto con le classiche aspettative. La grande varietà di condizioni ambientali che tipicamente caratterizza le golene, generate dall'alternarsi di siccità e inondazioni, ha probabilmente prevalso sugli effetti della concorrenza. Inoltre, le differenze misurate sui girini, legate al tipo di habitat, hanno mostrato chiaramente che la scelta dell'habitat acquatico per la deposizione delle uova influenza la prestazione fisica dei girini. Riassumendo, la scelta differenziata dell'habitat avviene con ogni probabilità in ogni stadio del ciclo vitale degli anfibi e localmente facilita la coabitazione di specie dal ciclo vitale complesso.

Implicazioni per la protezione degli anfibi. I risultati di questo studio possono essere applicati per la protezione degli anfibi sia nel loro habitat acquatico che in quello terrestre. Abbiamo osservato che la selezione di nicchie differenziate da parte di specie diverse, sia nell'habitat acquatico sia in quello terrestre, avviene più facilmente se le condizioni ambientali subiscono variazioni importanti. La presenza di condizioni ambientali diversificate è quindi localmente un elemento fondamentale per la coabitazione di un'alta diversità di specie, in nicchie differenziate. Eventi che disturbano l'ecosistema, quali siccità o inondazioni, mantengono le condizioni ambientali molto variate. E' dunque importante che un certo grado di "disturbo naturale" possa avere luogo, al fine di mantenere il gradiente ambientale necessario a garantire un'elevata biodiversità.

Abbiamo osservato che detriti legnosi di grandi dimensioni giocano un ruolo determinante nella dimensione dell'*home-range* terrestre e rappresentano un elemento favorevole per entrambe le specie studiate, poiché forniscono un rifugio termico e una protezione dai predatori. Prelevare legname per utilizzarlo oppure per regolare il regime idrico, riducendone così la disponibilità, costringe gli anfibi a cercare rifugio in ambienti meno ideali. Questo causa un aumento della mortalità e quindi una diminuzione della popolazione di rospi. La disponibilità di grandi detriti legnosi nei rami secondari del fiume Tagliamento dipende dal bosco golenale adiacente e da un regime idrico dinamico. Laddove un fiume viene riportato a uno stato più naturale, torna ad aumentare la disponibilità di detriti legnosi e nel contempo si forma la diversità strutturale dell'habitat, necessaria per l'esistenza degli anuri negli habitat terrestri.

La *performance* dei girini, parametro importante nella conservazione di una popolazione, è apparsa migliore negli stagni ampi, poco profondi, caldi e a basso rischio predatorio, dei rami secondari del fiume. Se il letto del fiume, il regime idrico e la morfologia del corso d'acqua sono naturali, la successione vegetale non può stabilirsi, permettendo la conservazione dell'habitat. Ecco perché la rinaturazione dei fiumi è una strategia promettente: essa permette la formazione e la conservazione di quelle condizioni ambientali caratteristiche dei primi stadi della successione, che sono favorevoli ai girini. Questo non significa che gli stagni che si trovano a uno stadio avanzato della successione naturale, nel bosco golenale, non siano importanti per lo sviluppo dei girini. Al contrario, gli stagni del bosco golenale sono maggiormente protetti in caso di inondazioni, e in tale circostanza possono contribuire, anche se marginalmente, alla crescita della popolazione. Nei rami secondari del fiume, infatti, un'inondazione può significare una catastrofe per gli anuri. Tutti i tipi di stagni hanno un ruolo importante nello sviluppo e nella conservazione della popolazione di anuri. Il perimetro da considerare per la rinaturazione di un corso d'acqua deve dunque comprendere anche il bosco golenale adiacente.

INTRODUCTION AND THESIS OUTLINE

Behavioral activities of most animals are restricted to areas that are considerably smaller than expected from observed levels of mobility - the so called home-ranges. Home-ranges accommodate all behaviors related to reproduction and survival (Burt 1943) and are defined as the area repeatedly traversed by animals during their daily activities (Kenward 1985). Accordingly, Darwin (1861) noted that "…most animals and plants keep to their proper homes, and do not needlessly wander about; we see this even with migratory birds, which almost return to the same spot". That animals restrict their activities to home-ranges has fundamental consequences on habitat selection (Rhodes et al. 2005), which in turn affects population dynamics (Kjellander et al. 2004; Wang and Grimm 2007), and hence species diversity (Fagan et al. 2007) and co-existence of species.

In this context, differential habitat selection is considered a key process that stabilizes co-existence of species through spatiotemporal partitioning of habitats and resources (Chesson 2000; MacArthur and Levins 1967; Rosenzweig 1991). Identifying the factors that promote co-existence of species has been a central debate in ecology for decades (Gause 1934; Gliwicz and Wrzosek 2008; Hairston 1951; Hairston 1980; Hutchinson 1959; Pianka 1967). The main controversy has been on the importance of biotic vs. abiotic processes in controlling the local and regional co-existence of species. For example, do competitive interactions exclude species from their potential ranges (Gause 1934; Hardin 1960) or are species ranges more affected by predation risk (Gallet et al. 2007; Jiang and Morin 2005; Menge and Sutherland 1976)? Abiotic constraints surely limit the distribution patterns of species (Chesson 2000; Connell 1979; Dunson and Travis 1991; Matias et al. 2007); but how important are abiotic factors at the local scale? In attempts to explain distribution patterns across large areas some success has even been made by assuming that all species are ecologically equivalent (e.g. "neutral") (Hubbell 2001; Muneepeerakul et al. 2008; Tilman 2004).

We postulate that most ecological and abiotic processes that determine co-existence occur at local scales, i.e. within- and among those habitat patches that are within the range of individual habitat choice. It is at this local scale, rather than regional scale, where alternative processes proposed to explain species co-existence are best studied (Enright et al. 2007). With this thesis I aim to shed more light on the mechanisms underlying the co-existence of species with complex life cycles. Thereto, I studied both individual variation in terrestrial home-range size, terrestrial habitat selection as well as the selection of aquatic breeding habitats by pond-breeding anurans. Moreover, I quantified larval performance, which allowed to explore the fitness-consequences of aquatic habitat selection.

Life cycle and life history

Pond-breeding amphibians have a complex life cycle, with aquatic egg and larval stages, and terrestrial juvenile and adult stages (Wilbur 1980) (Fig. 1). Fertilization of eggs occurs at breeding sites. Larvae hatch within days to weeks. Larvae go through metamorphosis before entering the terrestrial stage, and this life history transition is associated with a change in behavior and ecology. The time spent in the aquatic habitat is short, compared to the time spent in the terrestrial habitat (Fig. 1). Larval growth and size are regulated interactively by a variety of abiotic and biotic factors out of which, hydroperiod length, temperature, predation risk, and competition are most important (Morin 1986; Wellborn et al. 1996; Wilbur and Collins 1973). Size at metamorphosis is a fundamental trait that affects survival and fecundity in later life (Altwegg and Reyer 2003; Berven 1990; Rieger et al. 2004; Semlitsch et al. 1988). The expectation is that large-sized metamorphs benefit from higher juvenile and adult survival as well as higher fitness compared to small-sized metamorphs.

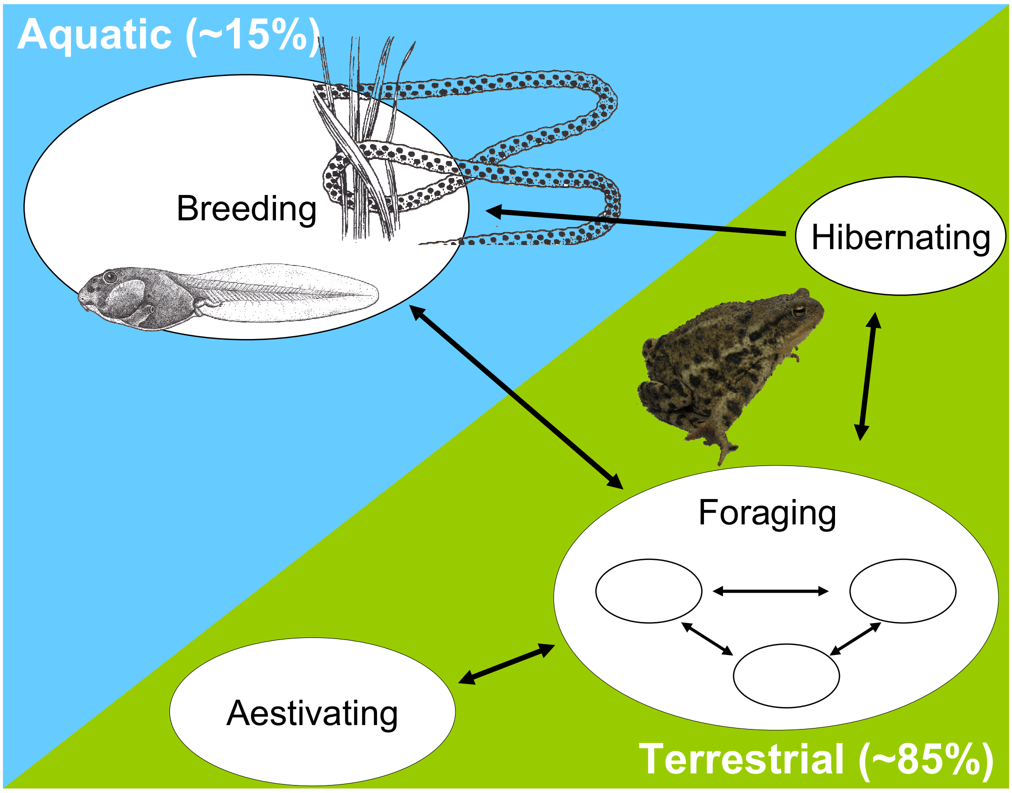

Figure 1. Illustration of the life cycle of pond-breeding amphibians (modified after Semlitsch (2003a). Egg and larval development depend on the aquatic environment and is completed within e.g. 8 weeks (~15% of the time of a year). The terrestrial juvenile and adult stage integrates behaviors such as resting, foraging, aestivating, and hibernating and encompasses approximately ~85% of the time of a year.

Reproductive adults of pond-breeding species spend most of their life time in terrestrial habitats, except water frogs and species from the genus *Bombina*. The terrestrial period includes behaviors such as aestivating, resting, foraging, and hibernating (Fig. 1). During summer, amphibians need abundant food to build up fat reserves for maintenance and future reproduction, as well as thermal and predatory refugia (Schwarzkopf and Alford 1996; Seebacher and Alford 2002; Wälti and Reyer 2007). That amphibians spend most of their life time in terrestrial habitat suggests that the abundance and species diversity of amphibians is most affected by processes occurring in the terrestrial habitat (Lampo and De Leo 1998). However, processes occurring at the larval stage surely affect population growth as well (Pechmann and Wilbur 1994; Semlitsch 2003b; Wilbur 1980; Wilbur and Collins 1973). Accordingly, recent evidence suggests that life time fitness is affected by processes occurring at both the larval and the terrestrial stage (Schmidt et al. 2008). These results indicate that knowledge on the habitat requirements of all life history stages is needed to develop conservation strategies for species with complex life cycles (Gibbs 2000; Marsh and Trenham 2001; Semlitsch and Bodie 2003).

Study system

The present study was conducted in the pristine dynamic floodplain of the Tagliamento River in northern Italy. It is an expansive braided floodplain river that retains the dynamic nature and morphological complexity that must have characterised most Alpine rivers in the pristine stage (Ward et al. 1999). Dynamic floodplains have almost completely disappeared as a result of human activity and, nowadays, they are among the most endangered ecosystems worldwide (Nilsson et al. 2005; Olson and Dinerstein 1998; Tockner et al. 2008). As a consequence, amphibians are primarily found in secondary habitats such as isolated and disturbed wetlands as well as in man-made waterbodies (Waringer-Löschenkohl et al. 2001). Most knowledge about amphibian ecology stems from experimental studies or has been carried out in secondary habitats, but little is known about amphibians in their primary habitats. The Tagliamento River therefore offers the rare opportunity to investigate the behavior and dynamics of amphibian populations in their primary habitat, where the ecology and life history of many amphibian species most likely evolved. Our data could serve as a reference point to develop conservation strategies for amphibians in landscapes that were transformed by human activities.

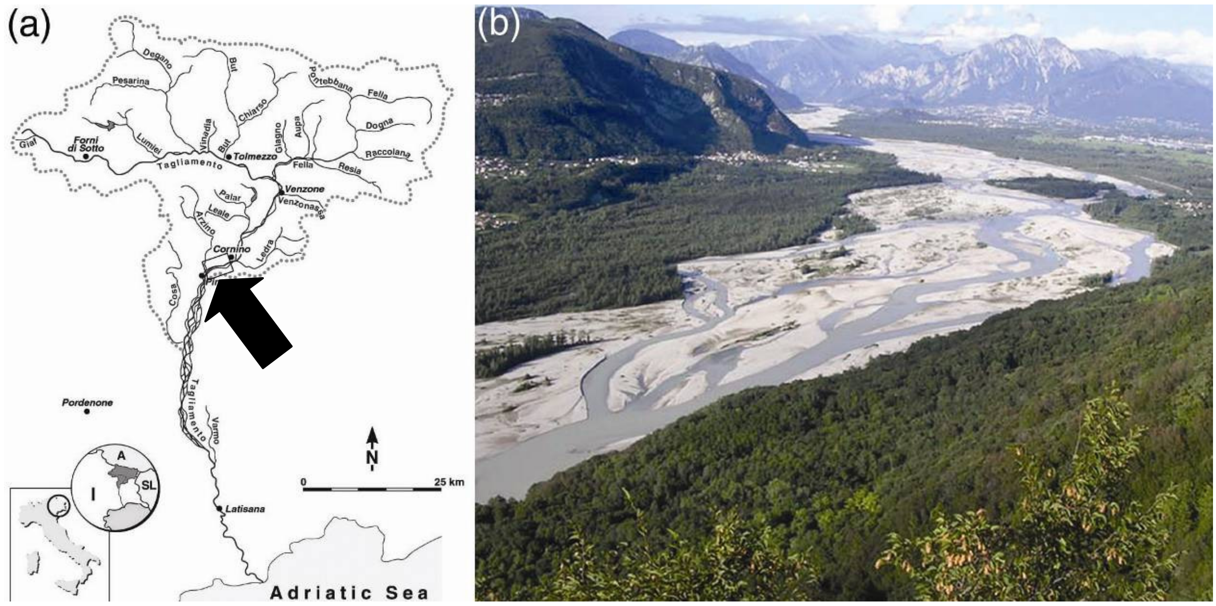

Figure 2. (a) Catchment map of the Tagliamento with location of major tributaries and towns. Inset shows the location of the catchment in Italy (I), near the borders of Austria (A) and Slovenia (SL) (modified after Ward et al. 1999). The main study area is indicated by the black arrow. (b) Oblique photo of the study site, taken from Monte Ragogna.

The Tagliamento floodplain is composed of two major habitat types, the active tract and the fringing riparian forest (Arscott et al. 2002; Petts et al. 2000). Regular droughts and floods result in predictable differences in hydroperiod length, predation risk, and temperature between the main habitat types (Wellborn et al. 1996). Ponds in the active tract are more variable in hydroperiod because of high infiltration loss; they contain less predators because of frequent drying and flooding; and they are more sun-exposed and hence warmer than ponds in the riparian forest. These environmental gradients may facilitate niche differentiation and hence co-existence of anurans in both the aquatic and the terrestrial habitat.

The study site (river-km 79.8 -80.8; 135 m asl) covered a 800-m wide active tract and the adjacent riparian forest (right bank). The active tract comprised a spatiotemporally complex mosaic of vegetated islands, a braided network of main and secondary channels, backwaters and ponds, embedded within a matrix of exposed gravel sediments (Petts et al. 2000) (Fig. 2). Within the riparian forest ponds are distributed along an abounded alluvial channel. This river section was chosen because both habitat heterogeneity (Arscott et al. 2002) and amphibian diversity are high (Tockner et al. 2006) and because the studied species were abundant across the floodplain. Furthermore, ponds were patchily distributed in the dynamic floodplain and the distances among ponds were far below the range of dispersal distances of the species studied. This was an important precondition to separate the effects of competitive interactions and geographic distances between ponds on species' occurrence (see chapter 4).

Study species

Out of 20 species from the regional species pool (Giacoma and Castellano 2006) eleven were present in our 1.6 km^2 large study section (Tockner et al. 2006). The four most abundant anuran species were the European common toad *Bufo bufo spinosus*, the Green toad *B. viridis*, the European common frog *Rana temporaria*, and Italian Agile frog *R. latastei*. *B. b. spinosous* and *R. latastei* were the pre-dominant species, followed by *B. viridis* and *R. temporaria* (Fig. 2). *B. viridis* occurred only in the active tract of the floodplain while other species occurred in both the active tract and the riparian forest. These species were used to study either breeding site selection (chapter 4), variation in home-range size (chapters 1 and 2), terrestrial habitat selection (chapter 3) and larval performance (chapter 5). Having species differing in life history and ecology was an important precondition to shed light on the mechanisms that may facilitate local co-existence of species.

Bufo b. spinosus is a ubiquitous species that typically spawns in permanent natural and man-made ponds in early spring (Giacoma and Castellano 2006). *Rana temporaria* is a widespread species that occurs across a wide altitudinal range. In Italy, *R. temporaria* is often found in cool wooded areas adjacent to running waters (Giacoma and Castellano 2006). *Rana latastei* is a characteristic lowland species that prefers vegetated ponds containing subsurface structures for egg attachment (Giacoma and Castellano 2006). However, *R. latastei* also spawns in temporary ponds in open areas. *Bufo viridis* is a pioneer species preferring warm and shallow ponds of early succession stages (Giacoma and Castellano 2006).

The frogs (*R. temporaria, R. latastei*) start breeding in February, followed by *B. b. spinosus* in March, and by *B. viridis* in late April. The breeding period of frogs is constrained to few weeks. *Bufo b. spinosus* extends the breeding period from weeks to months depending on the predictability of the environment (Kuhn 1993). Similarly, *B. viridis* colonizes ponds that fill at high water level until late July (L. Indermaur, *personal observation*).

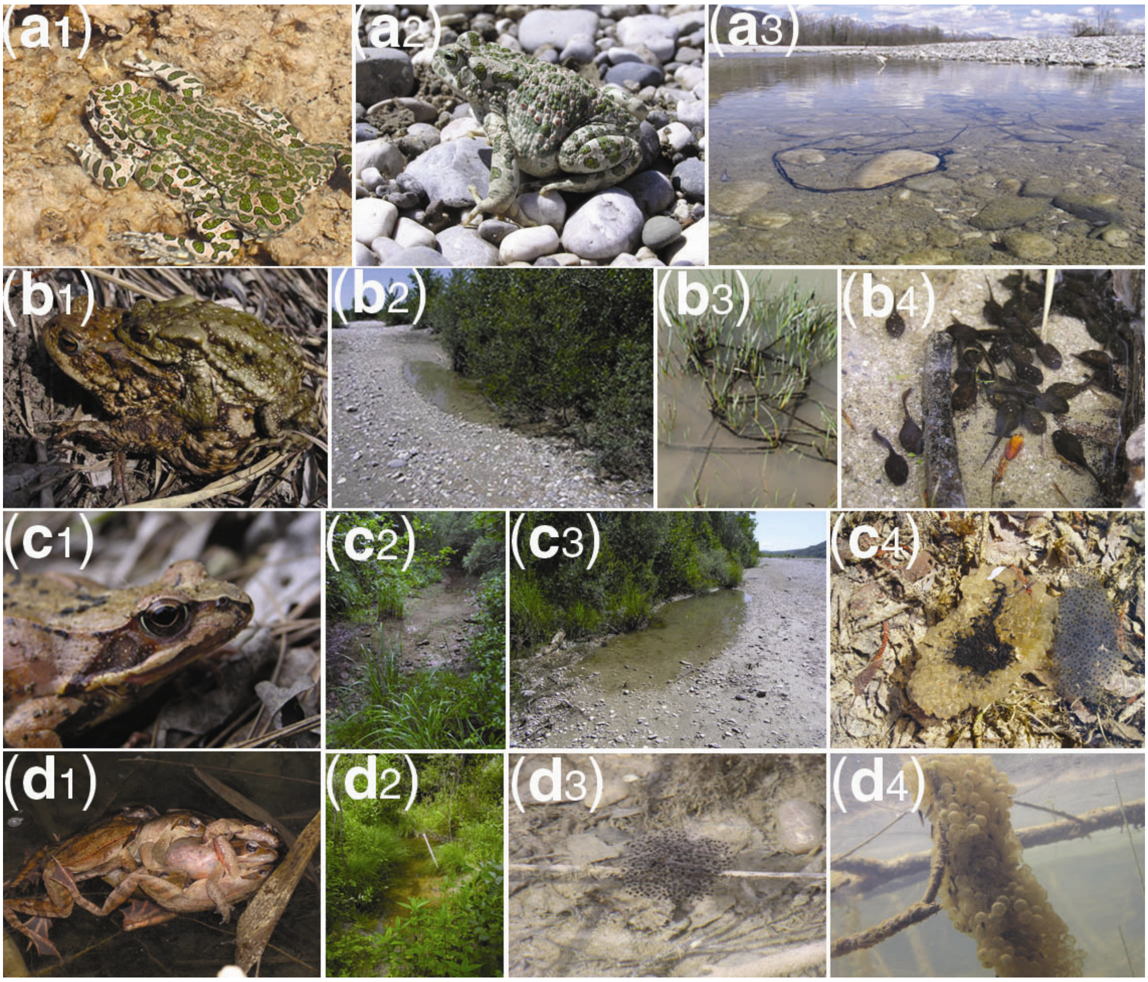

Figure 2. Impression of terrestrial adult and aquatic egg and larval stages of study species as well as their characteristic breeding sites The Green toad (*Bufo viridis*) at (a_1) breeding sites and in the (a_2) terrestrial summer habitat. (a_3) egg clutch of *B. viridis* in a shallow side channel containing no structural elements for egg attachment. (b_1) Couple of the European common toad (*B. b. spinosus*) on its way to breeding sites. Females may carry males over large distances. (b_2) characteristic breeding site of *B. b. spinosus*, associated to vegetated islands within the active tract; (b_3) egg clutches and (b_4) larvae. (c_1) The common frog (*Rana temporaria*), characteristic breeding sites in the (c_2) riparian forest and (c_3) the active tract. (c_4) egg clutches of *R. temporaria*, differing in age (left: old clutch with hatchlings; right: new clutch). (d_1) Many males of the Italian Agile frog (*R. latastei*) compete for a single female. (d_2) characteristic breeding site of *R. latastei* in the riparian forest. (d_3, d_4) egg clutches of *R. latastei*, differing in age. Egg clutches of *R. latastei* are always attached to structural elements such as twigs and branches. Species were used to study (a_1, b_1) variation in home-range size and the selection of terrestrial summer habitat; (a_1,b_1,c_1,d_1) breeding site selection and (b_1) larval performance.

Thesis goals and outline

With this thesis I aimed to fill some voids regarding our understanding of aquatic and terrestrial amphibian ecology. By studying both aquatic and terrestrial habitat requirements, we hoped to shed more light underlying the co-existence of species with complex life cycles.

The presented thesis consists of five chapters. Chapters 1 to 3 are devoted to terrestrial amphibian ecology that is the study of variation in home-range size (chapter 2) and habitat selection (chapter 3) as well as methodological issues (chapter 1). Chapters 4 and 5 are devoted to aquatic amphibian ecology that is the selection of breeding sites (chapter 4) and larval performance (chapter 5). The quantification of both aquatic and terrestrial habitat selection allowed to explore whether differential habitat selection is evident in both the larval and the adult stage, thereby facilitating co-existence of species with complex life cycles. The quantification of larval performance (chapter 4) allowed the exploration of whether breeding site selection was a fitness-relevant process.

Chapter 1. During tracking studies, the behavior of animals may be affected by the tracking and tagging methods used, which may influence the results obtained. The aim was to assess the impact of transmitter mass and the duration of tracking period on the body mass change of two anuran species (*Bufo b. spinosus* and *B. viridis*) that were fitted with externally attached radio transmitters during the terrestrial summer period. We evaluated whether body mass change is rather affected by environmental factors (temperature, prey density) than methodological factors (transmitter mass, tracking duration, and the sum of distances between consecutive locations, which is a surrogate for energy expenditure). This was an important step to evaluating potential bias in the results presented in Chapters 2 and 3.

Chapter 2. Understanding variation in individual home-range size remains a major issue in ecology, and it is complicated by definitions of spatial scale and the interplay of multiple factors. We explored why animals restrict their behaviors to areas that are considerably smaller than expected from observed levels of mobility – so called home-ranges. We asked, which factors control the size of terrestrial summer home-ranges of anurans, and does the impact of factors vary with the home-range definition (spatial scale) used? Essentially, we quantified the effect of habitat, biotic and individual factors on individual home-range size of the European common toad (*Bufo b. spinosus*) and the Green toad (*B. viridis*) that were radio-tracked in their terrestrial summer habitat. Analyses were done for two spatial scales that differed in their intensity of use: small 50% core areas within home-ranges with highest intensity of use, which is where animals spend 50% of their time, and large peripheral areas of home-ranges (95%-home-ranges excluding the 50% core areas) with lower intensity of use.

During the summer period amphibians need abundant food to build up fat reserves for maintenance and future reproduction, as well as thermal and predatory refuge. Hence, resting and foraging are the dominating behaviors in summer. Resting may be confined to small areas whereas larger areas are required for foraging. And, these behaviors may segregate spatially because of non-overlapping distributions of food and shelter. We therefore expected that toads use the interior core areas of their home-ranges (50% core areas) for resting while they use the peripheral areas of 95% home-range (excluding 50% core areas) for foraging. Based on these assumptions we formulated three hypotheses that were expected to apply to both species: (H1) Habitat factors (habitat structure, home-range temperature) control the size of 50% core areas; (H2) biotic factors (prey density and competition) control the size of 95% home-ranges; and (H3) the effects of individual factors (body mass, sex, animal identity) on 50% core areas and 95% home-ranges are outweighed by habitat and biotic factors. The particular contribution of this study was our emphasis on behavior-based scale definitions because they facilitate the formulation of *a priori* hypotheses, thereby contributing to a better grounding of home-range studies in theory. Moreover, we showed how the interrelatedness of factors, which is typically inherent in field studies, can be handled. Finally, the usage of two sympatric species differing in ecology allowed shedding more light on the processes structuring home-ranges as well as the mechanisms that may facilitate co-existence in terrestrial habitats.

Chapter 3. In the previous chapter we determined the factors affecting the dimension of home-ranges. Here, we asked, which factors determine the occurrence of species within the floodplain and within their home-ranges? Moreover, does the occurrence in terrestrial habitats vary across spatial scales? Specifically, we quantified the selection of terrestrial summer habitat by two sympatric amphibians (*Bufo b. spinosus* and *B. viridis*) as a function of the interactive effects of habitat type, as well as a biotic (prey density) and an abiotic resource (temperature). We applied a novel resource selection model, accounting for differences among individuals, at three spatial scales: a) home-range placement within the floodplain, b) space use within 95% home-ranges, and c) space use within 50% core areas. We hypothesized that home-range placement is determined by both prey density and temperature because they are essential factors in summer for both species (H1). Summer home-ranges integrate spacious foraging and confined resting behavior. We therefore hypothesized that habitat use within 95% of home-ranges is determined by prey density (H2) and within 50% of core areas by temperature (H3). Last, we predicted that the two species exhibit differential resource selection for shared habitat types across spatial scales (H4) because this would facilitate their co-existence.

Chapter 4. Co-existence has been a central debate in ecology for decades but the mechanisms that allow co-existence are still a heatedly disputed topic. Main paradigms of ecology have shifted between importance of inter- and intraspecific competition, predation and abiotic factors as determinants of community structure. Anuran communities allow examination of the importance of ecological vs. abiotic processes to explain local species co-existence. In anurans, previous studies have shown that breeding site selection by reproductive females has important fitness consequences for developing tadpoles. Differential habitat selection is considered to reduce competition and hence allow co-existence, but the question calls for a detailed analysis. Here, we quantified breeding site selection of two pond-breeding toads (*Bufo bufo spinosus, B. viridis*) and two frog species (*Rana temporaria, R. latastei*) in relation to the separate and combined effects of landscape composition, hydrogeomorphology, abiotic and biotic conditions in ponds scattered patchily on a dynamic floodplain.

Chapter 5. Body size at metamorphosis is a critical trait in the life cycle of amphibians that affects population dynamics through survival and fecundity in later life. Despite the heavy use of amphibians as experimental model organisms, we poorly understand the mechanisms causing variation in metamorphic traits under natural conditions. We quantified body size at metamorphosis of a patchily distributed population of *B. b. spinosus* tadpoles in ponds of the active tract and of the riparian forest in an unconstrained alpine floodplain. The quantification of habitat type-specific population density at metamorphosis allowed the evaluation of whether breeding site selection by reproductive females (chapter 4) is a fitness-relevant process. The main goals were i) to determine whether tadpole performance (body size at metamorphosis, growth rates) and population density at metamorphosis in the two main habitat types is different, and ii) to quantify the impact of various factors governing differences in larval performance between habitat types and among ponds in general. For the second question, our focus was on among-pond variation in body size at metamorphosis, an important life history trait for species with complex life cycles.

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CHAPTER 1

Effect of transmitter mass and tracking duration on body mass change of two anuran species

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Abstract. During tracking studies, the behavior of animals may be affected by the tracking and tagging methods used, which may influence the results obtained. Our aim was to assess the impact of transmitter mass and the duration of tracking period on the body mass change (BMC) of two anuran species that were fitted with externally attached radio transmitters. *Bufo b. spinosus* and *B. viridis* were radio-tracked for three months during summer in the active tract of a large gravel-bed river (Tagliamento River, NE Italy). Our results demonstrated that transmitter mass and the duration of the tracking period did not affect BMC of the two anurans in their terrestrial summer habitats because methodological factors poorly predicted variation in BMC. Therefore, we encourage the use of tracking methods in amphibian ecology.

Introduction

Terrestrial habitats are pivotal for the viability of amphibian populations because the majority of amphibians spend most of their time in these areas (Semlitsch, 1998; Trenham and Shaffer, 2005). However, studies have focused on breeding sites where many amphibians are observed easily. Recently, the ecology of amphibians in terrestrial habitats has become an area of active research, in part because of progress in tagging techniques (Naef-Daenzer, 1993; Naef-Daenzer et al., 2005), which has allowed the successful tracking of small animals such as amphibians (Miaud et al., 2000; Faccio, 2003; Schabetsberger et al., 2004; Leskovar and Sinsch, 2005; Pellet et al., 2006). Data obtained by tracking methods may improve our understanding of animal ecology, such as by identifying key habitats needed for mating, hibernating, thermoregulation, and escape from predators, at times and places where direct observations are not possible. However, tracking methods may affect animal behavior and bias other parameters of interest (e.g. population density, survival) (Paton et al., 1991; Reynolds, 2004).

In amphibians, short term effects of external tags were found to either increase movement activity on the first night after tag attachment (Langkilde and Alford, 2002) or decrease activity levels within a four hour observation period (Blomquist and Hunter, 2007). Both studies compared movements of tagged and untagged frogs held under laboratory (Langkilde and Alford, 2002) and under semi-natural conditions (Blomquist and Hunter, 2007). The recent laboratory experiment by Rowley and Alford (2007) implies tag-effects on activity levels of frogs (*L. leseuri, L. nannotis, L. genimaculata*) unlikely to persist one day after tag attachment. However, in the wild, effects of tag-attachment may interact with other environmental factors. In addition, negative effects of attachment of tags, such as increased energy expenditure (Hooge, 1991; Godfrey et al., 2002) and lowered survival, may appear after longer observation periods (Gauthier-Clerc et al., 2004). It is necessary to assess the effect of tracking on behavior in the wild for relevant time periods (Wilson and McMahon, 2007) because otherwise erroneous conclusions and incorrect management decisions might be drawn. Very few studies have assessed effects of tags on the behavior of free-ranging animals because it is usually impossible to study untagged animals for comparison (Cotter and Gratto, 1995; Hill et al., 1999; Wilson and McMahon, 2006). However, opportunities exist to quantify the relative effect of different methods on tagged animals in the wild.

We followed two toad species fitted with external radio transmitters (*Bufo b. spinosus*, *B. viridis*) during the non-breeding period in the active tract of a large braided gravel-bed river (Tagliamento River, NE Italy). Our aim was to quantify the impact of the transmitter mass and the duration of the tracking period on body mass change (BMC) of the toad species.

Methods

Study site and species

The study was conducted from the end of June through September of 2006 along the free-flowing Tagliamento River (7th order stream, 172 km length) in the eastern Alps in Italy (46° N, 12°30’ E) (Ward et al., 1999; Tockner et al., 2003). The main study area was the active tract (1.6 km^2) of an island-braided floodplain complex (river-km 79.8 -80.8 from the source; 135 m asl) (Petts et al. 2000). The active tract was dominated by exposed gravel sediments (41.6%), surface water (9.1%), and vegetated islands (5.6%). Riparian forest fringed the 800 m wide active tract (Fig. 1).

Bufo b. spinosus and *B. viridis* were selected because they differ in their habitat requirements (Günther and Podloucky, 1996; Giacoma and Castellano, 2006) and because they were abundant at the study site (Tockner et al., 2006).

Figure 1. Overview of the study site from Monte Ragogna (L. Indermaur, 2006).

Radiotracking

We radio tagged 23 individuals of *B. b. spinosus* and 28 individuals of *B. viridis* in 2006 and followed them on average longer than one month (median; range: *B. b. spinosus*: 32 d; 13.4-75.9 d; *B. viridis*: 32.4 d; 14.1-68 d). Radio transmitters LT2-351 (2 g) or LT2-392 (5 g) (Titley Electronics Ltd, Ballina, Australia) each attached to a beaded-chain belt made of aluminium (Ball Chain Manufacturing Co., NY) were fitted around the toads' waists (Rathbun and Murphey, 1996) (Fig. 2). The belt was coated with black Plasti-dip (PLASTI DIP International Inc., Blaine, Minnesota USA) to avoid lateral abrasion and to be more cryptic to predators. *B. viridis* was tagged only with 2 g transmitters because of their smaller body mass. *B. b. spinosus* was tagged either with 2.3 g or 5.5 g transmitters. As recommended by Richards et al. (1994), the transmitter mass, including the harness, did not exceed 10% of the body mass (mean ± SD: *B. b. spinosus*: 4.32 ± 1.51 %; *B. viridis*: 6.86 ± 0.94 %). See Appendix A for details on tracking success and failure.

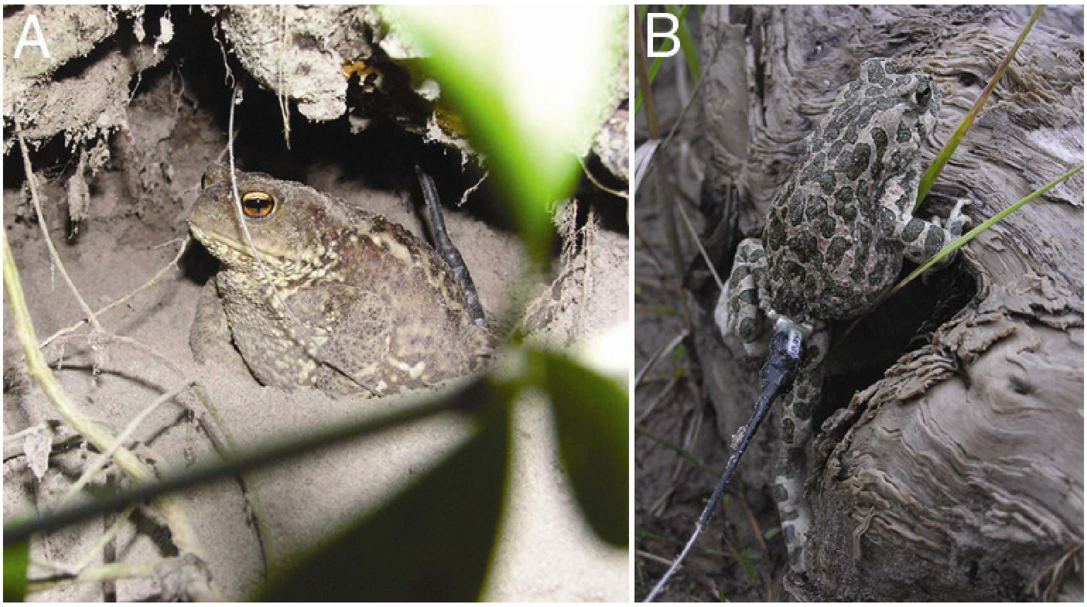

Figure 2. Common toad (*Bufo b. spinosus*) (A) hiding within an eroded bank and green toad (*Bufo viridis*) (B) emerging from a large wood deposit at sunset with externally fitted radio transmitter.

We used Australis 26k scanning receivers (Titley Electronics Ltd, Ballina, Australia) and hand-held three-element Yagi antennas (Model AY/C, Yagi collapsible) (Fig. 3A,B). At the start of the study, toads were weighed to the nearest 0.1 g, sexed, and snout-vent length was measured (Kuhn, 1997). All toads were re-weighed at weekly to biweekly intervals to monitor individual body condition (Fig. 3E). Toads were relocated six days a week, at day and at night. The position of the animals was recorded after homing in using a dGPS (average tracking resolution: 1 m) (Fig. 3C). Animals were not dug out to verify their presence when hidden under shelter for less than a week to avoid stress.

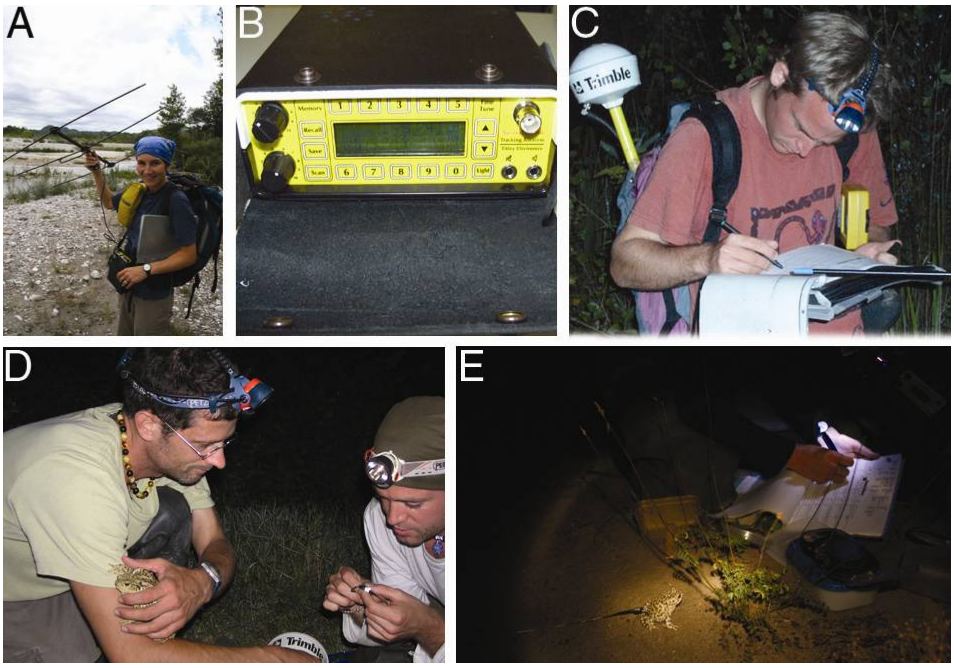

Figure 3. (A) Relocating of toads at daytime; (B) Scanning receiver; (C) Recording of spatial locations using dGPS as well as microhabitat descriptions and behavioral data; (D) Fitting of 5g-radio transmitter to a female of *Bufo b. spinosus*; (E) *B. viridis,* which has be re-weighed after 7 days.

Determinants of body mass

Apart from transmitter mass (2.3 and 5.5 g) and duration of the tracking period (number of tracking days per individual), a number of other factors may explain variation in BMC. These factors are body mass, body condition index (mass([g])/body length [mm]^3 10^6) (Hemmer and Kadel, 1972), surface temperature within the home-range, energy-expenditure, and prey density. We used these factors as alternatives that might better explain variation in BMC than transmitter mass or duration of the tracking period (Table 1).

Table 1. Candidate models used for predicting body mass change. All factors were standardized prior to analysis. Factor Sex was used in every model to correct for ist potential impact.

Model nr.	Model name	Factors		Explanation
1	global	Bc+Tw +T+E+Pr	+ D + M	all factors important
2	tracking period and body mass		+ D + M	body mass [g] at the beginning of the tracking period and tracking period [d] important
3	body condition	Bc	+ D + M	body condition index at the beginning of the tracking period important
4	transmitter mass	Tm	+ D + M	transmitter mass important (2 or 5 g)
5	temperature	T	+ D + M	habitat temperature important [°C]
6	energy-expenditure	E	+ D + M	Sum of distances between consecutive locations [m] moved important
7	prey	Pr	+ D + M	prey density important
8	tracking period		+ D	number of days [d] an individual was tracked important

Quantification of body mass determinants

All body mass determinants were quantified per individual home-range. We used 2684 locations *B. b. spinosus* and 2322 locations of *B. viridis* for the estimation of home-ranges (fixed kernels, 95% of locations, h = 0.3) using software "Ranges7" (Kenward and Hodder, 1996). See chapter 2 for further details on home-range estimation.

The body mass and body condition index were measured at the beginning of the tracking period. Home-range temperature was quantified using 57 temperature loggers (Thermochron ibuttons DS1921G, 0.5°C resolution, ±1°C accuracy from -30°C to 70°C) distributed in proportion to the aerial cover of individual habitat types. Temperature was logged at the sediment surface at hourly intervals. Average surface temperature within a home-range was calculated as the area-weighted mean of all habitat types within a specific home-range. Energy-expenditure per individual was expressed as the log-transformed sum of distances moved between consecutive locations. Prey density was quantified by exposing 100 pitfall traps (diameter 9 cm, depth 12 cm, volume 0.5 l) randomly along three transects perpendicular to the river course. The pitfall traps were sampled three times in 2006 (21-22 July, 8-9 August, 7-8 September), opened at twilight (8-9:30 p.m.) and closed at sunrise (around 5-7 a.m.). Assuming all pitfall content to be consumable by toads (Nöllert and Nöllert, 1992) we interpolated average prey density within the active tract by applying the inverse distance-weighted interpolation method in ArcGIS 9.0, using log-transformed prey densities (fit of the cross validated interpolation: $R^2 = 0.466$).

Statistical analysis

We applied the model selection approach proposed by Burnham and Anderson (2002) and Mazerolle (2006) to analyse among-individual variation in BMC. Eight candidate models (Table 1), each reflecting a specific hypothesis, were fit with general linear models (GLM) in R (Version 2.4.0; R Development Core Team 2005). All models, except model 8 had body mass and duration of the tracking period as covariates. This statistically removed the effect of these covariates when assessing the effects of other predictors (e.g. prey density). Model 4, using the factor transmitter mass, was not included in the model set of *B. viridis* because only 2.3 g transmitters were used. The importance of factors was evaluated by comparing the confidence intervals and the effect size of factors (Burnham and Anderson, 2002). One outlier (Cook's distance > 1) was removed. All factors were calculated per individual home-range and standardized (mean = zero, standard deviation = 1) prior to modelling. Tracked individuals that lost the transmitter before body mass was measured twice and without stable home-range size estimates were omitted for analysis.

Results

Bufo b. spinosus females weighed on average three times more than males (mean ± SD: 143.3 ± 37.8 g, *n* = 18; 52.0 ± 12.9 g, *n* = 6, respectively). In contrast, *B. viridis* females weighed only 13% more than males (mean ± SD: 30.5 ± 2.6 g, *n* = 20; 26.6 ± 5.6 g, *n* = 12, respectively). The body condition index at the beginning of the tracking period of *B. b. spinosus* was on average about 28% higher than of *B. viridis* (mean ± SD: *B. b. spinosus*: 121.5 ± 36; *B. viridis*: 86.9 ± 11.9). The initial body condition index of *B. b. spinosus* fitted with radio tags late in the season was higher compared to animals radio-tagged early in the season (mean ± SD: "early": 106.2 ± 15.8, *n* = 29, "late": 118.4 ± 40.2, *n* = 30). The opposite was true for *B. viridis* ("early": 96.9 ± 12.5, *n* = 26; "late": 91.9 ± 10.5, *n* = 28). The total distance travelled, a surrogate for energy expenditure, was larger for *B. viridis* (mean ± SD: 1061.7 ± 1191.2 m) than for *B. b. spinosus* (706.6 ± 915.4). During the study period, *B. b. spinosus* gained body mass (mean ± SD: 0.095 ± 0.519 g d^{-1}; *n* = 24) whereas *B. viridis* lost mass (0.443 ± 0.904 g d^{-1}; *n* = 32). Predation among all animals tracked in two years was low: out of 114 tracked *B. b. spinosus* 3 individuals (2.6%) were likely killed by herons or minks whereas out of 134 tracked *B. viridis* 8 individuals (5.9%) were killed by snakes (*Natrix natrix*).

For *B. b. spinosus* the prey-density model was clearly the best for explaining variation in BMC (Table 2). All other models received little support from the data.

Table 2. Model selection results for predicting body mass change (BMC), sorted after AICc differences (ΔAICc), for *Bufo b. spinosus* and *B. viridis*. The top-ranked model (bold) with ΔAICc=0 best explains the data. Models with ΔAICc ≤ 2 are considered to receive substantial support from the data. Coefficient of determination (R^2), number of parameters (K), log-likelihood (LL), Akaike's small sample information criterion (AICc), model weights (ωi) and evidence ratios (ER) are listed. ER are the ratios of model weight of a particular model in relation to the top-ranked model.

Model no.	Models	R^2	K	LL	AICc	ΔAICc	ωi	ER
	Bufo b. spinosus (n = 22)							
7	**prey**	0.488	5	-17.5	50.1	0.0	**0.999**	1
8	tracking period	0.164	3	-29.4	66.1	16.0	000.0	2976
3	body condition	0.246	5	-27.0	67.5	17.5	000.0	6171
2	tracking period and body mass	0.199	4	-28.9	67.9	17.9	000.0	7645
4	transmitter mass	0.231	5	-28.4	70.2	20.1	000.0	2.E+04
5	temperature	0.216	5	-28.7	70.7	20.6	000.0	3.E+04
6	energy-expenditure	0.207	5	-28.8	70.9	20.8	000.0	3.E+04
1	global	0.585	9	-14.7	73.2	23.1	000.0	1.E+05
	B. viridis (n = 28)							
1	**Global**	0.500	8	-26.9	79.4	0.0	**0.989**	1
7	Prey	0.382	5	-38.1	89.3	10.0	0.007	145
3	body condition	0.346	5	-39.0	90.5	11.1	0.004	259
8	tracking period	0.002	3	-47.1	101.0	21.7	000.0	5.E+04
2	tracking period and body mass	0.032	4	-46.6	102.7	23.3	000.0	1.E+05
6	energy-expenditure	0.077	5	-45.8	104.0	24.6	000.0	2.E+05
5	temperature	0.032	5	-46.6	105.5	26.1	000.0	5.E+05

However, prey density was not a reliable predictor because the 95% confidence interval included zero (Table 3). For *B. viridis*, the global model was best (ωi = 0.989) at predicting BMC (see Table 2). The body condition at the beginning of the tracking period had the largest effect (beta = 0.762) on BMC and best predicted variation in BMC (Table 3).

Table 3. Effect size (Beta, i.e. slopes of factors in general linear models), standard error (SE), coefficient of variation (CV = SE / Beta), lower (LCI) and upper (UCI) confidence intervals, separated for both species. Important factors (CV values ≤ 0.5 or confidence intervals include zero) are given in bold. Betas are shown for the best selected model therefore values are missing for some factors. For abbreviations of factors see Table 1. All factors were standardized prior to analysis.

Factors	Beta	SE	CV	LCI	UCI
B. b. spinosus					
E					
T					
Tm					
Pr	0.101	0.180	1.784	-0.259	0.460
Bc					
M	-0.123	0.191	1.555	-0.504	0.259
D	0.324	0.176	0.543	-0.028	0.677
B. viridis					
E	0.205	0.156	0.759	-0.106	0.516
T	0.009	0.337	37.024	-0.665	0.683
Pr	-0.008	0.230	27.127	-0.468	0.451
Bc	**0.762**	**0.193**	**0.253**	**0.376**	**1.147**
M	0.325	0.206	0.634	-0.087	0.737
D	-0.107	0.167	1.561	-0.441	0.227

There was weak evidence that energy expenditure explained variation in BMC. However, this predictor has to be considered with caution because its confidence intervals included zero. Animals with a higher body condition index at the beginning of the tracking period increased their body mass over time.

Discussion

Our results provided no indication that the external attachment of tracking devices affected BMC of *B. b. spinosus* and *B. viridis* because both the duration of the tracking period and the transmitter mass (evaluated only for *B. b. spinosus*) poorly predicted variation in BMC (Tables 2 and 3). This result was consistent when repeating modelling with the larger data set (2005 and 2006: *B. b spinosus*: *n* = 47; *B. viridis*: *n* = 52) and without the prey-density model (L. Indermaur, *unpublished data*) (no prey density for 2005 available). In addition, we observed toads with tracking devices accessing dense vegetation and narrow shelters (mouse holes), burying themselves up to 30 cm into the sand, and shedding skin. We cannot rule out an effect of transmitter mass on the BMC of *B. viridis* because we used only 2 g transmitters for this species. As the duration of the tracking season had no impact on BMC of *B. viridis*, we consider a transmitter effect unlikely. If the transmitter mass were to have had an impact on the BMC of *B. viridis*, then that effect is likely to have increased with the duration of the tracking period. In addition, the low initial body condition index of individuals radio-tagged late in the season compared to individuals radio-tagged earlier suggested that BMC of *B. viridis* was a consequence of environmental conditions rather than methodological factors. This is in line with Sinsch et al. (1999) who showed the body condition of males of *B. viridis* in mid-summer to be lower than in the beginning of autumn. Females, however, varied less in their body condition for the same observation period.

In amphibians, the effect of tag attachment has been understudied, but appears to be minimal, supporting our results. Oldham and Swan (1992) showed that body mass fluctuations and feeding rates of *B. bufo* and *Rana temporaria* were unaffected by ingested transmitters weighing 2.5 g. Using laboratory experiments Langkilde and Alford (2002) showed externally diode-tagged hylid frogs (*L. leseuri*) to move almost three times further and 69% more often on the first night after tag-attachment compared to untagged individuals. Conversely, radio-tagged *R. pipiens* and *R. sylvatica* were shown to move slightly less within four hours compared to untagged animals (Blomquist and Hunter, 2007). However, the follow-up laboratory experiment by Rowley and Alford (2007) showed tag effects on activity levels in three diode-tagged hylid frogs (*L. leseuri, L. nannotis, L. genimaculata*) to decrease after a one-day acclimatisation period (Rowley and Alford 2007). This implied that effects of tags on activity levels are unlikely to persist. In addition, all three species maintained their body mass over the tracking period. In the present study we might have increased the stress level of animals because they were repeatedly handled for weighing or harness adjustments. Nevertheless, we do not believe our results to be biased because the factor duration of the tracking period, integrating repeated handling, was unsupported by the data. To evaluate the discomfort of tracking devices on animals, stress indicators such as heart rate and respiration rate were recommended (Wilson and McMahon, 2006). However, these stress indicators would have required repeated surgical interventions for replacing batteries, if the same individuals were supposed to follow for longer periods. To fully understand the effects of tracking devices and repeated handling on animal behavior one would need control groups without tags and/or without handling. This is almost impossible in a field study.

We provided further evidence that the body condition of two toad species was unaffected by tag attachment under field conditions and for a relatively long observation period. This implies that tracking does not affect amphibian behavior under the condition of our study. Our results might hold also for amphibian species carrying other types of externally attached tags, such as diodes.

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Appendix A. Evaluation of tracking success and failure.

We conducted a pilot study in 2004 on 10 individuals of *Bufo bufo bufo* that were radio-tracked from the end of June until the beginning of September and located once at day and night to evaluate the performance of transmitters. Adult toads were fit with radio transmitters LT2-351 (2g) or LT2-392 (5g) (Titley Electronics Ltd, Ballina, Australia). The life span of transmitters was about 10 weeks and 6 months, respectively. The detection range varied between 10 m and 400 m, depending on the terrains' topography and animals' hiding place. When animals were buried underneath stones and fitted with transmitter LT2-351, the detection range was minimal. Signals of transmitters LT2-392 were consistently stronger than signals of transmitter LT2-351.

The transmitters were tightly fitted with an aluminium beaded-chain belt (Ball Chain Manufacturing Co., NY) around the waist (Rathbun and Murphey 1996) (Fig. 2). Animals either accepted the transmitter or tried to get rid of it by moving with outstretched legs. In the latter case, we quickly removed the transmitter. The beaded-chain belt caused lateral abrasions on every second animal during the pilot study. When the abrasions did not heal after loosening the belt we removed the radio-transmitter. In 2% of the relocations, the antenna was entangled in dense vegetation and animals had to be manually released. The radio-transmitters were modified in this respect for the main study, i.e. we attached less flexible antenna to avoid entangling in dense vegetation.

For the main study in 2005 and 2006 in Italy, the belt was coated with black Plasti-dip (PLASTI DIP International Inc., Blaine, Minnesota USA), a silicon-like substance, to avoid lateral abrasion and to be more cryptic to predators. The coating of the belt clearly avoided abrasions: out of 114 individuals of *B. b. spinosus* and 134 individuals of *B. viridis* that were ever fit with a radio-transmitter, 1 individual of *B. b. spinosus* (1%) and 5 individuals of *B. viridis* (4%) had lateral abrasions. We removed the transmitter from these animals and excluded them from analyses. Three individuals of *B. viridis* became snagged on vegetation by the belt and were manually released. We lost the signal of three individuals of *B. b. spinosus*, and two individuals of *B. viridis*, likely due to transmitter failure. We removed the transmitter from all animals at the end of the study period.

The transmitter did not limit the toads' ability to access narrow shelters (mouse holes), to burry themselves up to 30 cm into the sand, and to shedd skin. No other effect on the toads' behavior was observed. Animals were not dug out to verify their presence when hidden under shelter for less than a week to avoid stress and bias in movements.

Over two years (2005-2006) 7417 locations on 114 *B. b. spinosus* and 134 *B. viridis* were gathered. For estimation of home-range size, we used 6071 locations of 67 *B. b. spinosus* and of 59 *B. viridis*. Thus, 41% of all radio-tracked individuals of *B. b. spinosus* and 56% of *B. viridis* were omitted for analyses because they lost the transmitter before a sufficient number of locations was collected to robustly estimate home-range size. Sixteen animals that lost the transmitter were recaptured and fitted again with radio-transmitters. These animals were identified by individual photos that were taken at first capture.

Predation among all animals tracked in two years was low: out of 114 tracked *B. b. spinosus* 3 individuals (2.6%) were likely killed by herons or minks whereas out of 134 tracked *B. viridis* 8 individuals (5.9%) were killed by snakes (*Natrix natrix*). Two individuals of *B. viridis* died, likely due to desiccation.

CHAPTER 2

Behavior-based scale definitions for determining individual space use: requirements of two amphibians

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Abstract. Understanding individual space use remains a major issue in ecology, and it is complicated by definitions of spatial scale and the interplay of multiple factors. We quantified the effect of habitat, biotic and individual factors, on space use by amphibians (*Bufo b. spinosus* BB, *Bufo viridis* BV) that were radio-tracked in their terrestrial summer habitat. We analyzed two spatial scales, 50% core areas and 95% home-ranges (excluding 50% core areas), thought to represent resting or foraging areas, respectively. The 50% core area of BB was best explained by habitat structure and prey density, whereas the 50% core area of BV was determined solely by habitat structure. This suggests that the resting and foraging areas of BB are not spatially separated. The 95% home-range of BB was determined by prey density, while for BV both habitat structure and prey density determined home range size.

We conclude that the terrestrial area requirements of amphibians depend on the productivity and spatiotemporal complexity of landscapes and that differential space use may facilitate their co-occurrence. Behavior-based a priori hypotheses, in combination with an information theoretic approach and path analyses, provide a promising framework to disentangle factors that govern individual space use, thereby advancing home-range studies.

Introduction

Home-range size, accommodating all behaviors related to reproduction and survival (Burt 1943), has been used as an indicator of energy expenditure (Schoener 1968) and animal performance (Kenward 1985). These factors are in turn linked to key parameters of population dynamics. For example, with decreasing home-range size, population density and dispersal rate are predicted to increase (Kjellander et al. 2004, Wang and Grimm 2007). Thus, home-range size is a general variable for studying spatially structured populations, and it is informative for population management (Lomnicki 1988).

Among species, variation in home-range size is strongly related to body size (McNab 1963, Biedermann 2003). Among individuals, variation in home-range size may be influenced by food availability and competition (Ebersole 1980), predation risk (Lima and Dill 1990), cover (Tufto et al. 1996), and differences among individuals (Börger et al. 2006*b*). Furthermore, habitat structure, e.g. habitat composition, configuration, and connectivity, is related to the distribution of resources and shelter (Prohl and Berke 2001). However, the effects of habitat structure and resources on home-range size have rarely been disentangled (but see Tufto et al. 1996, Lombardi et al. 2007). Habitat structure *per se* may constrain or facilitate access to resources (Arthur et al. 1996, Revilla et al. 2004), and the distribution of the preferred habitat type may have a dominating effect on space use (Pasinelli 2000, Buner et al. 2005), suggesting a close link between habitat selection and home-range size. In this study, we therefore include factors for overall habitat structure (e.g. habitat richness) and partial habitat structure (area of preferred habitat type) and food resources to quantify their separate effects on home-range size.

Home-range size is usually quantified using a single spatial scale, e.g. the area including 95% of either raw locations or a calculated utilization distribution (Worton 1989). Animals, however, do not use home-ranges uniformly. The intensity of use is higher within core areas than in the peripheral parts of the home-range, which may reflect the spatial segregation of behaviors (Marzluff et al. 2001). Consequently, the ecological relevance of the key underlying factors may vary with spatial scale (Börger et al. 2006*b*). Hence, we need multiple spatial scales when quantifying variation in home-range size. We propose to define the spatial scales at which to study variation in home-range size by the behaviors they likely integrate. This novel approach allows the formulation of *a priori* hypotheses on how the impact of factors is expected to vary with scale and behavior, facilitating our understanding of spatially structured populations.

Dynamic floodplains comprise a spatially complex habitat mosaic (Naiman et al. 2005) and are therefore good model systems to study the impacts of habitat factors (e.g. habitat richness, temperature) and biotic factors (food resources) on individual space use. We used two amphibian species (common toad *Bufo b. spinosus* and green toad *B. viridis*), differing in life history and ecology, to shed more light on the processes structuring terrestrial summer home-ranges. The two toad species co-occur within the active tract of a naturally dynamic floodplain (Tockner et al. 2006). Our main goal was to quantify direct and indirect effects of habitat, biotic, and individual factors on the size of 50% core areas and 95% home-ranges.

We focus on the terrestrial summer period because of its importance for the viability of amphibian populations (Trenham and Shaffer 2005, Rittenhouse and Semlitsch 2007) and because it narrows the set of factors that influence space use. During the summer period amphibians need abundant food to build up fat reserves for maintenance and future reproduction (Wälti and Reyer 2007), as well as refugia from desiccation (Schwarzkopf and Alford 1996, Seebacher and Alford 2002). Hence, resting and foraging are the dominating behaviors in summer that may segregate spatially. We therefore expect that toads use the 50% core areas within home-ranges for resting while they use the peripheral areas of 95% home-range (excluding 50% core areas) for foraging. Based on these assumptions we formulated three hypotheses that are expected to apply to both species.

1. Habitat factors (habitat structure, home-range temperature) control the size of 50% core areas. We expect the 50% core areas to decrease with increasing habitat structure (e.g. area of large wood, habitat richness) (Kie et al. 2002, McLoughlin et al. 2003, Buner et al. 2005), as well as to decrease with increasing temperature (Schwarzkopf and Alford 1996, Seebacher and Alford 2002).

2. Biotic factors (prey density and competition) control the size of 95% home-ranges. We expect the size of 95% home-ranges to decrease with increasing food density and competition (McNab 1963, Hixon 1980).

3. The effects of individual factors (body mass, sex, animal identity) on 50% core areas and 95% home-ranges are predicted to be outweighed by habitat and biotic factors. Body mass is likely a poor explanatory factor as fluctuations in body mass are primarily caused by evaporation and adsorption of water rather than by food intake. The reproductive status (sex) (Lombardi et al. 2007) and differences among individuals (Steury and Murray 2003) are considered less important during the non-breeding season.

Our emphasis on behavior-based *a priori* hypotheses for determining space use by individuals contributes to a better grounding of home-range studies in theory. The statistical approaches applied here, provide a promising analytical framework to untangle the web of factors that govern space use, thereby advancing our understanding of spatially structured populations.

Methods

Study site

The study was conducted from mid-June until the end of September 2005 and 2006, along the 7th order Tagliamento River in northeastern Italy (46° N, 12°30’ E). The Tagliamento (catchment area: 2,580 km^2) originates at 1000 m asl in the southern fringe of the European Alps and flows almost unimpeded for 172 km to the Adriatic Sea. The river retains its natural morphological and hydrological characteristics.

The main study area was the active tract (1.6 km^2) of an island-braided floodplain complex (river-km 79.8 -80.8; 135 m asl). This reach contains a spatially complex and temporally dynamic habitat mosaic embedded in an extensive matrix of exposed riverine sediments (Petts et al. 2000) (see chapter 1, Fig. 1).

The 800 m wide active tract is bordered by riparian forest on the north bank, and the steep hillslope of Monte Ragogna on the south bank. Further detailed information on the Tagliamento catchment and the main study area can be found elsewhere (Ward et al. 1999, Arscott et al. 2002, Tockner et al. 2003).

Study species

Bufo b. spinosus is a generalist species associated with densely vegetated habitats, while *B. viridis* is a pioneer species of the continental and Mediterranean steppes (Giacoma and Castellano 2006). *B. viridis* is a quick colonizer of pioneer habitats and far more versatile than *B. b. spinosus*. Both toad species may burrow to withstand harsh environmental conditions and for hydration (Hoffmann and Katz 1989). *B. b. spinosus* is considered less tolerant to high temperature than *B. viridis* (Degani et al. 1984, Meek and Jolley 2006).

Habitat mapping

In 2005 and 2006, the entire study area was mapped in detail at base flow (about 20 m^3 s^{-1}) using a differential GPS (Trimble GeoXT, Zurich), and data were processed using ArcView GIS 9.0 (ESRI, Redlands, California, USA). Seven habitat types were discriminated: exposed gravel sediments (63.9 ha; averaged values for both years), water (13.5 ha), established islands (woody vegetation > 2 m tall, topographically elevated, ≥ 1 m^2; 8.3 ha), open pioneer vegetation (cover 10% to ≤ 50%; 6.3 ha), dense pioneer vegetation (cover > 50%; 3.9 ha), large wood deposits (≥ 0.5 m^2; 1.2 ha), and eroded banks (ecotones of established islands providing many earth holes as refuges, with slopes between 45 and 90°; 0.3 ha).

Radio telemetry

Adult toads were caught during random searches at night, weighed, and fitted with radio transmitters LT2-351 (2g) or LT2-392 (5g) (Titley Electronics Ltd, Ballina, Australia). The transmitters were tightly fitted with an aluminium beaded-chain belt (Ball Chain Manufacturing Co., NY) around the waist (Rathbun and Murphey 1996) (see chapter 1, Fig. 2).

The mass of the transmitter, including the belt, did not exceed 10% of the body mass (mean ± SD: *B. b. spinosus*: 4.32 ± 1.51 %; *B. viridis*: 6.86 ± 0.94 %), as recommended by Richards et al. (1994). At the start of the study, all toads were sexed and photographed to allow individual identification if a transmitter tag was lost. All toads were re-weighed to the nearest 0.1 g at weekly to biweekly intervals during the study period to monitor individual body condition. Neither transmitter mass nor duration of the tracking period negatively affected changes in the toads' body mass (Indermaur et al. 2008).

Scanning receivers (Australis 26k) and hand-held antennas (Yagi Model AY/C, Yagi collapsible) were used for tracking the toads (Titley Electronics Ltd, Ballina, Australia). We followed each of 56 radio-tagged *B. b. spinosus* and 59 *B.*

viridis between one and three months (*B. b. spinosus*: mean 44.5 d, range 13.4-99.5 d; *B. viridis*: mean 33.1 d, range of 13.5-71 d). The exact position of each toad was recorded six days a week, once at day and night, using a GPS (average tracking resolution: 1 m). Two observers simultaneously located toads in different parts of the study area, randomly varying the tracking time and the sequence of tracked animals. For more details on the telemetry methods, see chapter 1, Fig. 3, Appendix A.

Estimation of home-range size

For home-range estimation, a total of 3079 locations of *B. b. spinosus* and 2545 locations of *B. viridis* were collected (mean number of locations ± SD: *B. b. spinosus*: 55 ± 27.6; *B. viridis*: 43 ± 16). A preliminary analysis (incremental plots: Hayne 1949) of the relationship between the number of locations and home-range estimates showed that 20 locations of *B. b. spinosus* and 25 locations for *B. viridis* were required to obtain robust individual home-range size estimates. Because the number of locations was at least twice as high as the calculation locations, we consider that our estimates were robust.

Fixed kernel home-ranges were calculated with “Ranges 7” (grid: 160 x 160 cells, cell size: 1 m^2), using the 50% or 95% contours of the density distribution (South et al. 2005). We omitted the outer 5% of the data. Their inclusion would have extended contours into areas that were not repeatedly used for daily activities but rather explorative behavior, thereby introducing bias in home-range size estimates (Kenward 2001). Toads were considered to use the interior core of home-ranges for resting, and their periphery for foraging, depicted by the 50% contour and the 95% contour, respectively. These spatial scales were discriminated for each species separately by applying a regression of probability of use against the proportion of total area (Fig. 1) (Clutton-Brock et al. 1982, Powell 2000).

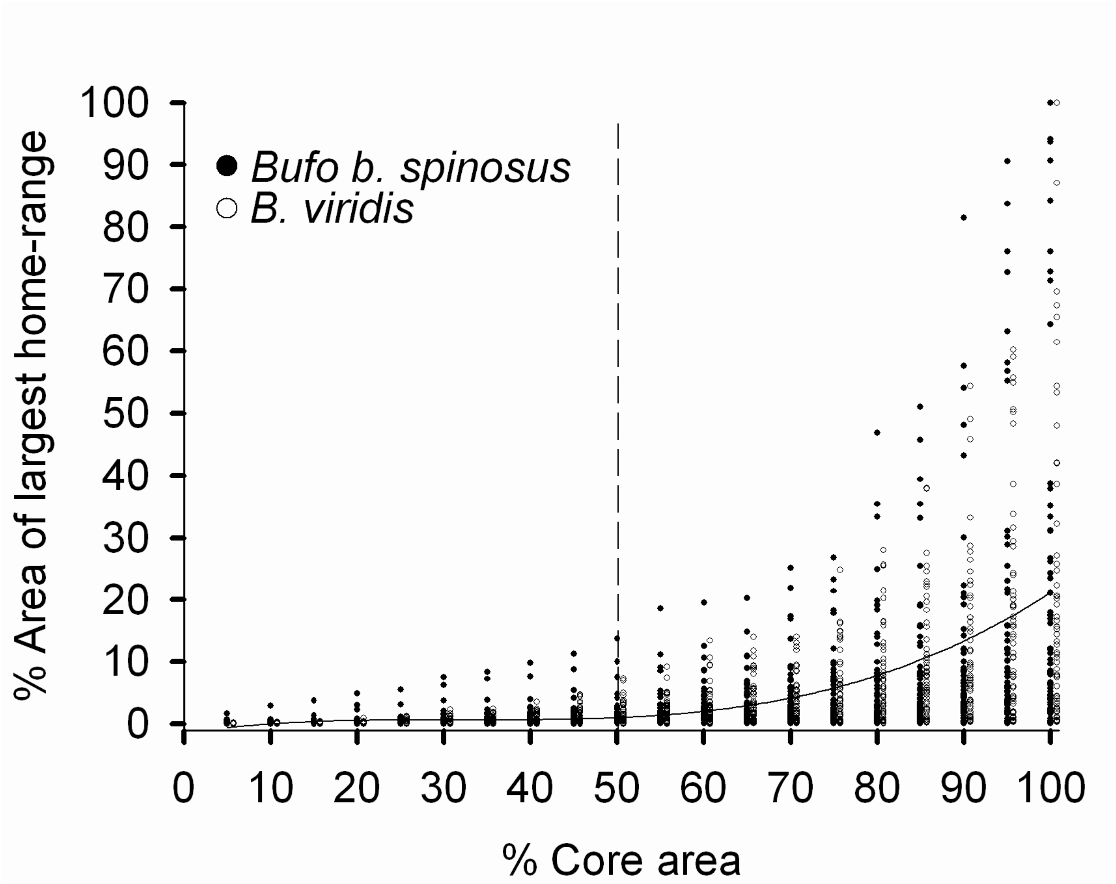

Figure 1. Estimates of % of core areas are plotted in 5%-intervals against the % area of the largest home-range for 2005 and 2006. The increase of the regression line after the 50% core area (vertical dashed line) denotes increased foraging activities.

The average smoothing factor (h = 0.3) was least-squares cross-validated using “Ranges 7”, validated by our field observations and applied to all individuals of both species . Because *B. viridis* avoided established islands and the riparian forest, we fitted the 95%-contours of *B. viridis* as such as they touched the boundary of these habitat types and compared the congruency of the empirically fitted contour with the analytically derived one using “Ranges7”. The contours were entirely congruent, therefore justifying the applied smoothing factor.

Determinants of home-range size

Home-range size was predicted using 3 habitat factors (habitat richness, area of large wood deposits, home-range temperature), 2 biotic factors (prey density, competition), and 3 individual factors (body mass, sex, animal identity) (Table 1).

Table 1. Habitat, biotic, and individual factors used for predicting home-range size.

Code	Factor
Habitat factors	
T	Home-range temperature [°C]
Ri	Habitat richness†
Wood	Area of large wood deposits†,‡
Biotic factors	
Co	Intra- and interspecific competition [m]
Prey	Prey density
Individual factors	
M	Body mass of animals at the beginning of the tracking period
Sex	Sex (integer)
A	Animal identity=Animal number (integer)

Note: All factors were standardized prior to analysis.

† Habitat richness and the area of large wood deposits were surrogates for habitat structure. Highly structured habitats were considered to provide more refuges for protection from harmful environmental conditions than would weakly structured habitats.

‡ Large wood deposits was the preferred habitat type within home-ranges (see analysis of habitat selection, Appendix A).

By applying a principle component analysis we *a priori* omitted additional explaining factors reflecting habitat structure because of redundancy or the lack of additional variance explained (Appendix B). Home-range temperature was quantified using temperature loggers (Thermochron ibuttons DS1921G, 0.5°C resolution, ±1°C). In 2005 we used 67 loggers, and in 2006 57 loggers, with an hourly logging interval and recorded temperatures at the sediment surface, with locations distributed in proportion to the aerial cover of individual habitat types. Average home-range temperature within a home-range was calculated as the area-weighted mean of all habitat types within a specific home-range.

Prey density was quantified in 2006 by setting up 100 pitfall traps (diameter 9 cm, depth 12 cm, volume 0.5 l) randomly along three transects perpendicular to the river corridor. The pitfall traps were sampled three times (21/22 July, 8/9 August, 7/8 September), and were opened (set) at twilight (8:00-9:30 p.m.), and closed at sunrise (5:00-7:00 a.m.). Averaged prey availability (number of prey items/m^2) within the active tract of the floodplain was calculated by applying the inverse distance-weighted interpolation method in ArcGIS 9.0 using log-transformed prey densities (fit of interpolation: R^2 = 0.466). Competition (intra- and inter-specific) was calculated by buffering the kernel center of a home-range with a diameter of 19 m (average 50% core area) or 45 m (average 95% home-range), and summing the weighted inverse distances to all other kernel centers within the buffer. The buffer distance was chosen to allow for home-range overlap between individuals.

Statistical analysis

Modeling strategy. We used an information theoretic approach (model selection) proposed by Burnham and Anderson (2002) and path analysis (Mitchell 1993) to quantify variation in home-range size. The information theoretic approach was used to fit a set of eleven candidate models from which we derived model-averaged effect sizes to evaluate the importance of explaining factors. Each of these models reflects a hypothesis with a sound basis in the literature (Appendix C). In contrast to the information theoretic approach, path analysis is helpful in quantifying both the direct effects of factors on a response variable, as well as their indirect effects on a response variable via intermediary factors. Hence, we quantified the indirect and direct effects of the most important home-range size determinants out of the information theoretic approach using path analysis to better understand the interrelatedness of factors. The information theoretic approach therefore served to set the theoretical background for the path models. To avoid redundancy, we focus on the path analysis and refer to appendices for methods and results out of the information theoretic approach (Appendices D-F). We assumed that the interior 50% core areas were mainly used for resting while the peripheral areas of the 95% home-range were mainly used for foraging. We therefore removed the 50% core area from the 95% home-range for modelling to avoid confounded results.

Path analysis. We fitted path models (AMOS 7.0; SPSS Inc., Chicago) separately per species and spatial scale (50% core area, 95% home-range). The direct effects were measured by the standardized partial regression coefficient between Y and Xj by holding all other factors constant. The direct effects were the path coefficients relating Y to Xj. This way, the path models controlled for nuisance correlations among factors typical in field studies. In the present study we *a priori* accepted the correlation between habitat richness, area of large wood deposits, home-range temperature, and prey density (Appendix G) because each factor may have its own merit. For modelling we used data from 2006 because prey density was not sampled in 2005. All factors were z-standardized prior to analysis. Home-range size was log-transformed to assure normally distributed residuals. One outlier (Cook's distance > 1) was removed.

Results

Home-range use: The percentage of locations toads were observed moving (= foraging) was consistently lower within 50% core areas than within 95% home-ranges (number of locations in % of total locations in 50% core areas/95% home-ranges: *B. b. spinosus*: 5.4/17.2; *B. viridis*: 9.3/40.2) (Appendix H). However, the percentage of total locations animals were seen moving at day was higher in the 50% core areas of *B. b. spinosus* than of *B. viridis*. These results indicate the interior core areas were used primarily for resting and that the peripheral areas of the 95% home-range mainly for foraging, but also that *B. b. spinosus* may forage to some extent as well in 50% core areas. However, our data do not allow further behavioral detail, such as commuting movements between resting and foraging areas, to be resolved

Home-range size, shape and overlap

The mean 50% core area and 95% home-ranges of *B. b. spinosus* were 48 m^2 and 570 m^2 respectively, and those of *B. viridis* were 295 m^2 and 2456 m^2, respectively (Table 2). The differences between the two species were statistically significant (50% core areas, univariate ANOVA: $F_{1,109} = 9.054$, $P = 0.003$, mean squared error [MSE] = 0.46; 95% home-ranges, univariate ANOVA: $F_{1,109} = 10.23$, $P = 0.002$, MSE = 0.433). Median home-range size was consistently smaller than mean home-range size (right-skewed distribution), hence few individuals had very large home-ranges (Table 2).

The 50% core areas were not significantly different between sexes ($F_{1,109} = 0.186$, $P = 0.667$, MSE = 0.46), and there was no interaction between species and sexes ($F_{1,109} = 0.180$, $P = 0.672$, MSE = 0.46). Similarly, the 95% home-ranges were not significantly different between sexes ($F_{1,109} = 1.713$, $P = 0.193$, MSE = 0.433), and there was no interaction between species and sexes ($F_{1,109} = 1.694$, $P = 0.196$, MSE = 0.433).

Table 2. Home-range size estimates and body mass (mean ± SD) for both toad species.

				50% core area [m^2]				95% home-range [m^2]				Body mass [g]	
Species	Year	Sex	*n*	Median	Mean	SD	Range	Median	Mean	SD	Range	Mean	SD
Bufo b. spinosus													
	2005	M+F	25	44	70	104	3 - 406	305	675	986	32 - 3620	123.4	51.9
	2006	M+F	29	19	29	37	3 - 191	160	480	766	6 - 3345	126.7	50.0
	2005/2006	M	11	26	37	32	3 - 104	533	1164	1354	32 - 3620	52.0	13.3
	2005/2006	F	43	24	51	86	3 - 406	210	418	638	6 - 3526	143.3	38.1
	2005/2006	M+F	54	24	48	78	3 - 406	230	570	872	6 - 3620	125.1	50.5
B. viridis													
	2005	M+F	23	95	124	130	4 - 568	820	1074	992	36 - 3899	30.8	5.8
	2006	M+F	36	86	404	1016	1 - 5000	1472	3339	4810	27 - 17248	28.0	4.6
	2005/2006	M	20	84	466	1126	1 - 5000	1337	3028	4470	36 - 13781	26.6	3.4
	2005/2006	F	39	91	208	578	1 - 3633	1109	2162	3677	27 - 17248	30.5	5.6
	2005/2006	M+F	59	91	295	806	1 - 5000	1204	2456	3946	27 - 17248	29.1	5.3

Note: M=males, F=females, *n* = number of animals, SD=Standard Deviatiation

For each species, virtually all 95% home-ranges were multi-nuclear, i.e. they consisted of spatially separated areas (see inset in Fig. 2).

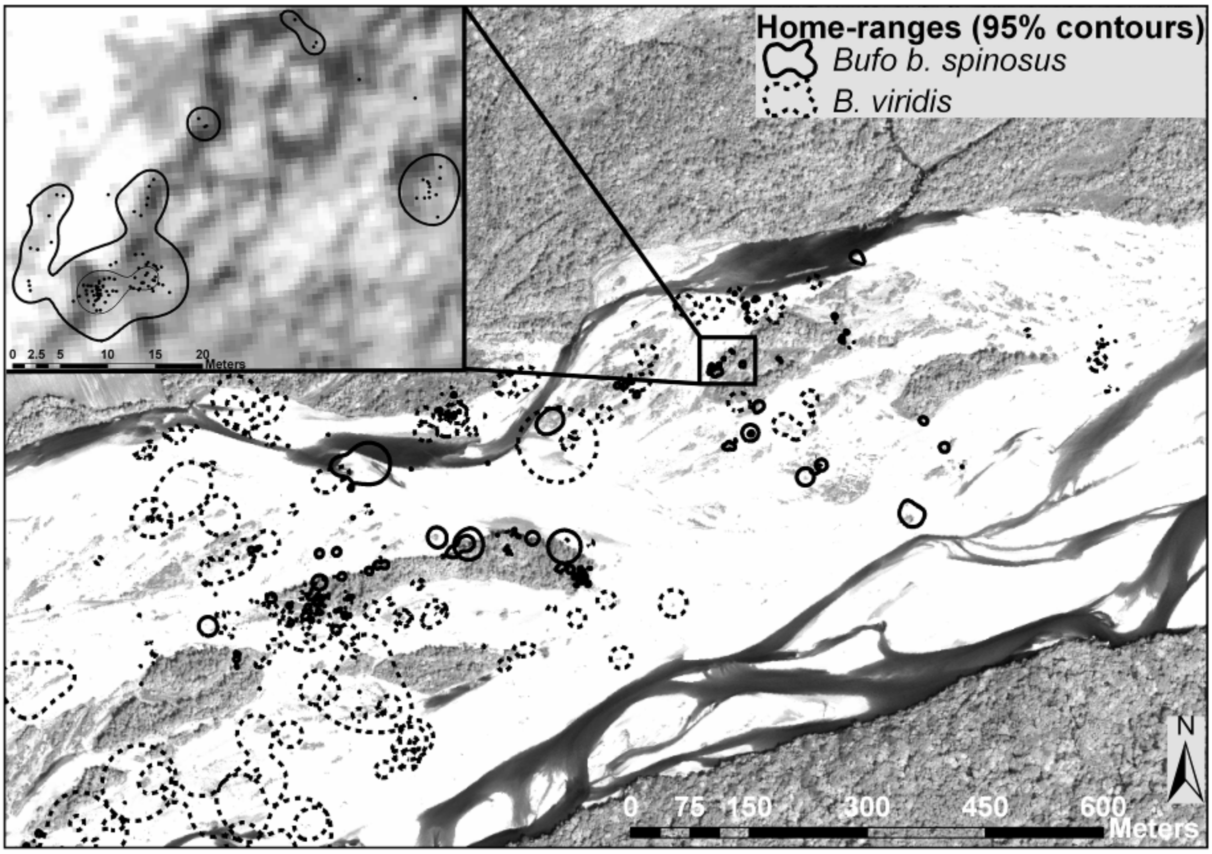

Figure 2: Part of the distribution of home-ranges (95% contours) of both species in the study site (2006 data). Riparian forest fringes the active tract, which is mainly composed of exposed gravel sediments (white), the river network (dark grey), and vegetated islands (pale grey). The upper left corner shows the multi-nuclear structure of one *Bufo b. spinosus* home-range (50% core area=thin line; 95% home-range=thick line) and the distribution of locations.

The relative (%) overlap of home-ranges between species was small (mean ± SD: 50% core areas: 0.33 ± 0.20%; 95% home-range: 2.67 ± 1.81%) as well as the relative overlap of home-ranges among individuals of a species (50% core area: *B. b. spinosus*: 0.34 ± 0.39%, *B. viridis*: 3.10 ± 2.86%; 95% home-range: *B. b. spinosus*: 2.75 ± 1.88%, *B. viridis*: 11.24 ± 6.18%).

Determinants of home-range size

The most important home-range size determinants out of the information theoretic approach were habitat richness, area of large wood deposits, and prey density (confidence intervals of regression coefficients did not include zero), all related to home-range temperature (Appendices D-F). Individual factors and the biotic factor competition (Table 1) were considered unimportant (confidence intervals included zero, see Appendices E,F). Hence, we used all habitat factors (habitat richness, area of large wood deposits, home-range temperature) and the biotic factor prey density to establish a path model, integrating the interrelatedness of factors, to explain variation in home-range size (Fig. 3).

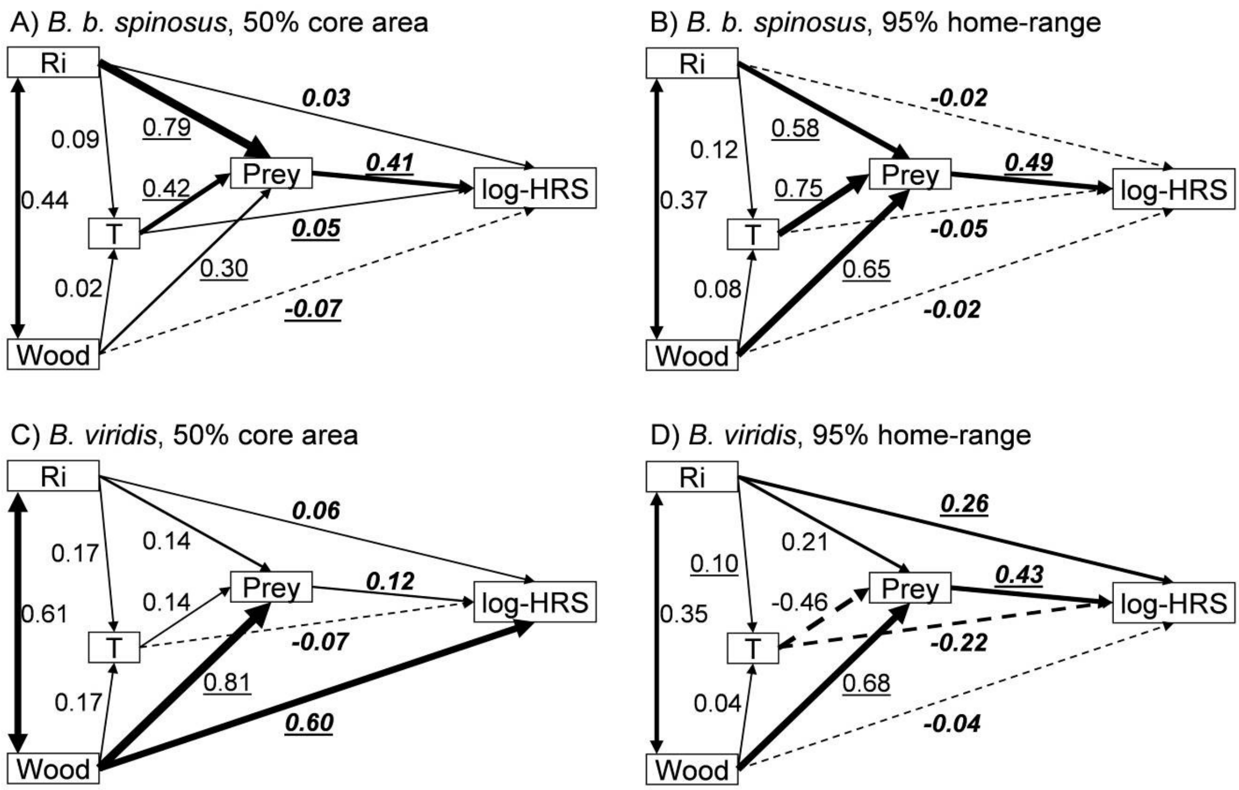

Figure 3: Path diagrams relating the factors habitat richness (Ri), area of large wood deposits (Wood), home-range temperature (T), and prey density (Prey) to log-home-range size (log-HRS), separately per species, 50% core area and 95% home-range. The values for standardized direct effects (bold text, cursive) and indirect effects (normal text) are given adjacent to the arrows. The thickness of arrows is proportional to the effect size of factors. Significant effects are underlined (see Table 3 for significance levels). Negative relationships are shown in broken lines. Single headed arrows represent causal effects, double sided arrows represent correlations.

Via the direct path, we predicted that all habitat factors (habitat richness, area of large wood deposits, temperature) and the biotic factor prey density *per se* may affect home-range size. Via the indirect path, we predicted that habitat richness and the area of large wood deposits alter habitat temperature and therefore prey density, which in turn might indirectly affect home-range size. Factors reflecting habitat structure (habitat richness, area of large wood deposits) explained most variation in log-home-range size followed by prey density and temperature (Table 3).

Table 3. Effect sizes (Beta) and variances (R^2) with standard errors (SE) for the path models (see Fig. 3)

	50% core area					95% home-range				
Factors	Beta	SE	*P*	R^2	SE	Beta	SE	*P*	R^2	SE
Bufo b. spinosus (*n* = 23, GFI = 0.345)						*Bufo b. spinosus* (*n* = 22, GFI = 0.356)				
Direct effects										
Ri	0.030	0.017	0.078	0.762	0.023	-0.018	0.027	0.501	0.754	0.233
Wood	-0.074	0.110	<0.001	0.523	0.158	-0.017	0.035	0.634	0.406	0.125
T	0.052	0.017	0.002	0.114	0.034	-0.045	0.041	0.269	0.160	0.049
Prey	0.409	0.014	<0.001	0.071	0.021	0.493	0.028	<0.001	0.255	0.079
e3				0.001					0.004	0.001
Indirect effects										
Ri → T	0.087	0.115	0.452			0.119	0.135	0.379		
Ri → Prey	0.788	0.092	<0.001			0.577	0.174	<0.001		
Wood → T	0.020	0.139	0.883			0.079	0.184	0.667		

Wood → Prey	0.301	0.110	0.006			0.646	0.234	0.006		
T → Prey	0.421	0.168	0.012			0.754	0.275	0.006		
B. viridis (*n* = 24, GFI = 0.318)						*B. viridis* (*n* = 28, GFI = 0.489)				
Direct effects										
Ri	0.057	0.067	0.393	0.990	0.292	0.258	0.076	<0.001	0.905	0.242
Wood	0.597	0.103	<0.001	0.788	0.233	-0.042	0.093	0.648	0.828	0.221
T	-0.073	0.144	0.614	0.094	0.028	-0.217	0.295	0.462	0.042	0.011
Prey	0.123	0.091	0.176	0.235	0.069	0.435	0.085	<0.001	0.489	0.131
e3				0.045	0.013				0.099	0.027
Indirect effects										
Ri → T	0.088	1.925	0.054			0.100	0.044	0.024		
Ri → Prey	0.151	0.946	0.344			0.206	0.165	0.211		
Wood → T	0.099	1.723	0.085			0.039	0.046	0.395		
Wood → Prey	0.167	4.853	<0.001			0.682	0.161	<0.001		
T → Prey	0.331	0.438	0.661			-0.462	0.648	0.476		

Note: See Table 1 for abbreviations of factors. All factors were standardized prior to analysis. *P* = P-value for significance level 0.001, e3 = unexplained variance in log-home-range size, GFI = goodness of fit index for the most constrained model. Values < 0 and > 1 indicate that the data do not fit the model while values close to 1 indicate good fit (Jöreskog and Sörbom 1984). The true model fit here lies somewhere between the GFI-values reported and 1.

Both direct and indirect effects controlled log-home-range size of both species (Fig. 3). The 50% core areas and 95% home-ranges of both species increased with the direct effect prey density (Table 3, Fig. 3). The direct effect of habitat richness was positively related to home-range size, except for the 95% home-range of *B. b. spinosus*. Home-range size decreased with the area of large wood deposits and temperature, except for the 50% core area of *B. viridis*. Temperature decreased with home-range size, except for the 50% core area of *B. b. spinosus*.

For *B. b. spinosus*, habitat richness and the area of large wood deposits had a significant effect on prey density while for *B. viridis* solely the area of large wood deposits had a significant effect on prey density (Fig. 3). Prey density increased with increasing habitat structure and temperature, except for the 95% home-range of *B. viridis*, where prey density was inversely related to temperature.

In the 95% home ranges, prey density and the area of large wood deposits varied less for *B. b. spinosus* than it did for *B. viridis* (Fig. 4). Average prey density in densely vegetated habitats (established islands, dense pioneer vegetation), mainly occupied by *B. b. spinsous* (Fig. 2), was about twice as high (359 individuals/m^2/d vs 183 individuals/m^2/d) than in open habitats (exposed gravel sediments) that were mainly occupied by *B. viridis*.

Prey availability was dominated by ground dwelling insects (% insect density for densely vegetated habitats/exposed gravel sediments: *Coleoptera*: 38.4/24.3; *Arachnidae*: 21.5/38.2; *Acarina*: 8.8/0; *Collembola*: 7.0/7.7) while exclusively flying insects (*Hymenoptera*: 7.4/7.2) contributed marginally to total density.

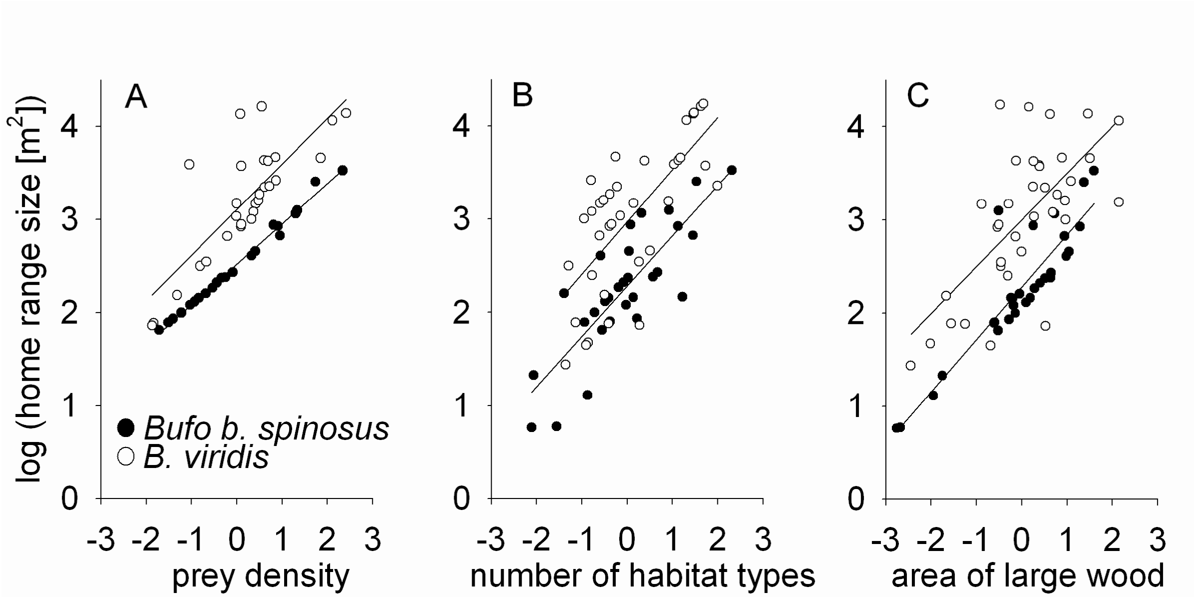

Figure 4. Relationships between log-home range size (95% home-range) and A) prey density, B) number of habitat types (habitat richness), and C) area of large wood deposits. Standardised values are shown. The relationships in figure 4 deviate partly from those in figure 3 due to the exclusion of other explaining factors and their interrelatedness.

Hypothesis 1: Habitat factors control the size of 50% core areas

For *B. b. spinosus*, the significant direct effects of both habitat factors (area of large wood deposits, temperature), and the biotic factor prey density determined its 50% core area (Fig. 3A), thereby partly supporting our hypothesis. The size of the 50 % core area decreased with increasing area of large wood deposits (Fig. 3A). The biotic factor prey density had the strongest direct effect on the size of 50% core areas.

For *B. viridis*, the direct effect of the habitat factor area of large wood deposits controlled its 50% core area (Fig. 3C), which is in line with our hypothesis. Other biotic, habitat, and individual factors were considered unimportant (Table 3,

Appendix E: confidence intervals include zero). Unexpectedly, the size of the 50% core area increased with increasing area of large wood deposits.

Hypothesis 2: Biotic factors control the size of 95% home-ranges

For *B. b. spinosus*, the biotic factor prey density solely determined its 95% home-range (Fig. 3B). Hypothesis 2 was partly supported, as the biotic factor competition poorly explained variation in its 95% home-range and as the size of the 95% home-range increased with increasing prey density (Table 3, Fig. 3B).

For *B. viridis*, the direct effects of the factors habitat richness and prey density controlled the size of its 95% home-range, thereby partly constituting our hypothesis. The 95% home-ranges were largest when both habitat richness and prey density were high.

Hypothesis 3: The effects of individual factors are outweighed by the effects of habitat and biotic factors.

All individual factors were poorly supported as indicated by the results out of the information theoretic approach, thereby confirming our hypothesis (Appendices D,E). Sampling bias, expressed by either the number of locations collected (Appendix E) or the number of weeks toads were tracked (Appendix F) poorly explained variation in home-range size (confidence intervals included zero). The direct effect sizes evaluated using path analysis (Table 3, Fig. 3), were similar to those evaluated with the information theoretic approach (Appendix E).

Discussion

Our main goal was to quantify the separate direct and indirect effects of habitat, biotic and individual factors on summer home-range size of amphibians (*B. b. spinosus* and *B. viridis*) at biologically relevant spatial scales: namely 50% core areas which are the interior areas of home-ranges with the highest intensity of use, and 95% home-ranges including large peripheral areas (about 10 times the size of 50% core areas). We hypothesized that (H1) the 50% core areas are mainly used for resting and therefore controlled by habitat factors reflecting refuge density (habitat richness, area of large wood deposits), while (H2) the 95% home-ranges (excluding the 50% core areas) are used for foraging and therefore controlled by biotic factors (prey density, competition). Furthermore, (H3) the impacts of individual factors on 50% core areas and 95% home-ranges were hypothesized to be marginal compared to habitat and biotic factors.

Our results demonstrate that a web of habitat and biotic factors determines summer home-range size of both species. However, the two species responded differently to the same web of factors when using 50% core areas and 95% home-ranges.

The impact of direct and indirect effects of habitat and biotic factors on space use

Direct effects: Our results demonstrate that the size of the 50% core areas and 95% home-ranges of two amphibians species, differing in life history and ecology, was primarily governed by habitat structure (habitat richness, area of large wood deposits) and prey density (food resources) (Table 3, Fig. 3). However, the generalist species *B. b. spinosus* responded to the area of large wood deposits and prey density within its 50% core area (Table 3, Fig. 3A) while the pioneer species

B. viridis solely responded to the area of large wood deposits (Table 3, Fig. 3C). These results suggest that *B. b. spinosus* may rest and forage within 50% core areas while *B. viridis* only rests within core areas, in line with behavioural field data (Appendix H). Furthermore, these results demonstrate the dominating effect of single habitat structures on space use, which has been shown for other animals, such as birds (Pasinelli 2000, Buner et al. 2005) and bears (McLoughlin et al. 2003).

For both species the 50% core areas increased with increasing habitat structure (surrogate for refuge density), except for *B. b. spinsous*, where the 50% core area decreased with increasing areas of large wood deposits (Fig. 3A,C). Hence, individuals may increase their core areas to include multiple habitat types (*B. b. spinosus;* Appendix E) or large wood deposits (*B. b. spinosus*, *B. viridis*) that are patchily distributed. A similar relationship was found by Tufto et al. (1996) and Rosalino et al. (2004) for roe deer and badgers. These results are in line with the resource-dispersion-hypothesis (Macdonald 1983), which predicts that home-range size increases when resources are patchily distributed. Hypothesis 1 was partly supported, as both habitat and biotic factors determined the size of the 50% core areas of *B. b. spinosus*.

The 95% home-range of *B. b. spinosus* was solely determined by the biotic factor prey density, which implies that this species forages in the peripheral areas of its home-range (Table 3, Fig. 3B). For *B. viridis,* habitat richness and prey density controlled the size of its 95% home-range (Table 3, Fig. 3D). *B. viridis* may therefore forage in more diverse habitats because of their higher productivity and/or because predatory shelters are located close to foraging areas in exposed gravel sediments. For example, rodents and ungulates reduced predation risk by decreasing distances between foraging places and shelters (Lagos et al. 1995, Hamel and Cote 2007). The patchy distribution of predatory shelters and prey as well as the depletion of food patches may have forced toads to extend their foraging areas, thereby increasing 95% home-ranges. The resulting multi-nuclear home-range structure (see inlet in Fig. 2), is most likely a general phenomenon in pond-breeding amphibians (Semlitsch 1981, Forester et al. 2006). In addition, large home-ranges are considered to mitigate the impacts of fluctuating environmental conditions (Ferguson et al. 1999), characteristic for dynamic floodplains (Arscott et al. 2001, Naiman et al. 2005). In contrast, small home-ranges (Table 2) might have resulted from the occasional spatial aggregation of food resources and refuge. Toads may stop adding areas to their home-ranges when minimum requirements are met. Therefore, increasing home-range size does not necessarily result in higher prey and refuge density.

The generalist species *B. b. spinosus* occupied densely vegetated habitats where prey density was about twice as high as in habitats mainly occupied by the pioneer species *B. viridis* (Fig. 2). The habitats of both species differed little in prey composition implying rather indiscriminate feeding habits of the two toads. Indeed, a number of studies showed prey selection by amphibians to depend on prey availability rather than prey size (Smith and Braag 1949, Berry 1970). In addition, individuals of the same amphibian species that differed largely in body size selected prey items of all sizes (Inger 1969). Hence, *B. viridis* might have increased its 95% home-range much more than *B. b. spinosus* to compensate for low prey density. This may explain the large differences in home-range size among species (Table 2) and suggests pioneer species may be more limited by prey density than generalist species.

Hypothesis 2 was partly supported, as the 95% home-range of *B. viridis* was determined by both prey density and habitat richness. However, competition was a poor predictor, although juveniles and undetected adults were excluded from our studies. Nevertheless, we consider our results robust. First, competition is most likely low under harsh environmental conditions (Intermediate Disturbance

Hypothesis; Connell 1979). Second, we radio-tracked a representative sample of the reproductive population (about 30% of *B. b. spinosus*, 60% of *B. viridis*), an estimate that is based on all individuals that were ever caught (chapter 1, Appendix A), on egg clutch counts over two years (L. Indermaur, *unpublished, data*), and by assuming equal sex ratios.

Indirect effects: Prey density increased with increasing habitat structure (habitat richness, area of large wood deposits) and mostly with increasing temperature (Fig. 3). However, prey availability for the generalist species *B. b. spinosus* was determined by overall habitat structure (habitat richness, area of large wood deposits), while prey availability for the pioneer species was determined by a single habitat structure (area of large wood deposits). Hence, both species used highly structured habitats because of their expected high productivity, as well as of their role as potential thermal and predatory refugia.

In general, home-range size decreased with increasing temperature, except the for the 50% core area of *B. b. spinosus*, where home-ranges were largest when temperature was high (Fig. 3). *B. b. spinosus* was exposed to moderate temperature in densely vegetated habitats (maximum: 33.5° C) whereas *B. viridis* was exposed to highest temperature in open habitats (maximum: 43° C). Hence, at high temperature *B. b. spinosus* may move and therefore forage more actively in its 50% core area (Appendix H). For *B. viridis*, which mainly rests in large wood deposits (Fig. 5) (mean maximum: 27.2° C), leaving thermal shelter may increase the desiccation risk, thereby decreasing movement activity and home-range size.

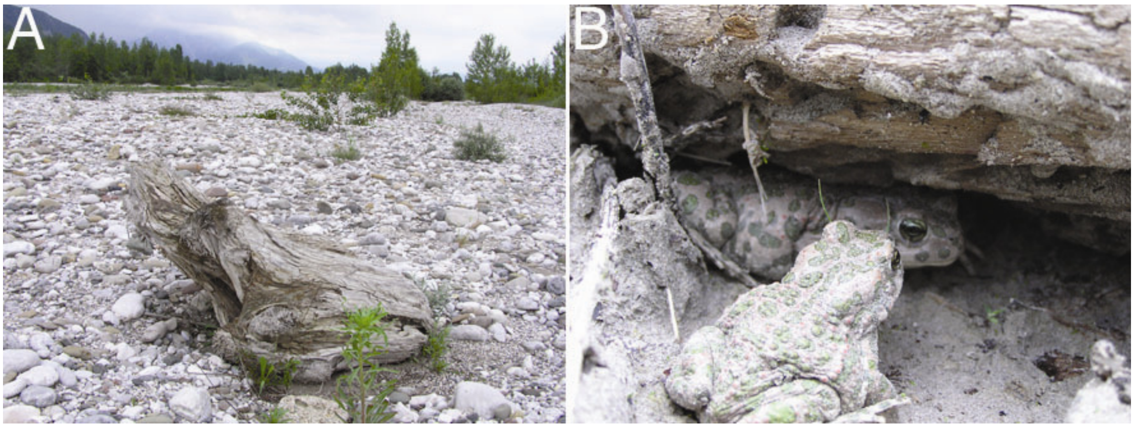

Figure 5. (A) Large wood deposit surrounded by exposed gravel sediments. (B) Two Green toads (*B. viridis*) emerging from the large wood deposit at sundown.

The impact of individual factors on space use

As expected (H3), individual factors poorly explained variation in 50% core areas and 95% home-ranges (Appendices D-F). The weak impact of body mass on 50% core areas and 95% home-ranges is in accordance with previous studies on deer (Relyea et al. 2000, Said and Servanty 2005) and bears (Dahle and Swenson 2003). We argue that in amphibians body mass strongly fluctuates due to evaporation and hydration, thereby masking changes in body fat. Furthermore, in patchy environments such as dynamic floodplains, metabolic requirements may not depend linearly on home-range size. Differences among individuals, expressed by the factor animal identity, was far less important than habitat and biotic factors (Appendices D-F), contradicting with experimental data on *Tribolium* beetles that were kept in micro-landscapes of varying complexity but stable environmental conditions (Morales and Ellner 2002). We expect that differences among individuals might be more important in less variable environments (Klopfer and MacArthur 1960).

Conclusions

We demonstrated that the summer home-range size (50% core areas and 95% home-ranges) of two pond-breeding amphibians was a function of prey density and habitat structure (habitat richness, area of large wood). Habitat factors directly affected home-range size, likely by increasing refuge density, or indirectly by increasing prey availability. This finding implies that the terrestrial area requirements of amphibians depend on the productivity and spatiotemporal complexity of the landscape. Reducing habitat complexity may therefore impede resting and foraging behaviors which are both paramount for survival and future reproduction (Wälti und Reyer 2007). The relative importance of the same factors varied between species and across spatial scales (50% core areas, 95% home-ranges). Therefore, differential space use facilitates the co-existence of the two toad species in the terrestrial summer habitat.

Our results did not fully correspond with the assumption that 50% core areas mainly integrate resting behavior as for *B. b. spinosus* the habitat factor area of large wood deposits (surrogate for refuge) and the biotic factor prey density determined the 50% core area. This suggests that resting and foraging behaviors may not be spatially separated. The use of behavior-related scale definitions therefore contributes to our understanding of spatially structured populations, regardless of whether underlying assumptions are met or not. Behavior-based scale definitions, applying an information theoretic approach, and path analysis provide a promising framework to disentangle the web of factors governing space use, and hence advance home-range studies.

Further research should focus in more detail on the relationships between habitat structure, resource density, and population dynamics. A number of empirical studies have shown that home-range size depends on habitat structure and/or resource density (Ebersole 1980, Prohl and Berke 2001, Buner et al. 2005, our study). Home-range size is generally predicted to decrease when population density increases (Kjellander et al. 2004, Wang and Grimm 2007). However, we lack empirical evidence that both home-range size and population dynamics are similarly controlled by the interplay of habitat structure and resource density. Approaching this topic would require an experimental setup where levels of habitat structure and resource density are easily manipulated, and the response (home-range size, population density) can be quantified. Another research direction should focus on the effect of qualitative differences (physiological state, tolerance to environmental factors) among individuals on home-range size in relation to environmental stability. As previously argued, theory predicts individual differences to be more important in stable rather than in dynamic environments (Klopfer and Macarthur 1960). As dynamic floodplains become more and more regulated and, therefore, habitat stability increases, differences among individuals might become more important in controlling home-range size. Furthermore, if there is evidence for individual differences, it is important to determine if these are related to survival and passed on to offspring.

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Appendix A. Ranking order of preferred habitat types from compositional analysis separated for both species and the 50% core area (50) and the 95% home-range (95). ERO=eroded banks, GRA=exposed gravel sediments, ISL=established islands, ISL-E=island edge (5 m buffer around established islands), LWD=large wood deposits, PD=dense pioneer vegetation, PL=open pioneer vegetation, RIP-E=riparian edge (5 m buffer along river network).

Species	Scale	1		2		3		4		5		6		7	*n*	λ	χ^2	*P*	d.f.
Bufo b. spinosus																			
	50	ERO	>	ISL-E	=	ISL	>	LWD	=	PD	>	GRA	>	PL	54	0.27	70.3	<0.001	6
	95	LWD	>	ISL-E	>	ERO	>	GRA	>	PD	>	ISL	>	PL	54	0.39	50.9	<0.001	7
B. viridis																			
	50	LWD	>>>	GRA	=	ISL-E	=	RIP-E	>	PL	>	PD	>	ERO	59	0.16	110.0	<0.001	6
	95	LWD	>>>	GRA	>	RIP-E	>	ISL-E	>	ERO	>	PL	>	PD	59	0.12	96.8	<0.001	6

Note: λ=Wilk's lambda, χ^2=chi square statistics, d.f. = degrees of freedom; >>> denotes a significant deviation, > a non-significant deviation from proportionality at $P < 0.05$.

Appendix B. Results of a principal component analysis summarizing variation in landscape measures, separated by species, the 50% core area, and the 95% home-range.

		50% core area		95% home-range	
		Component		Component	
Species	Factor	1	2	1	2
Bufo b. spinosus					
	Ri	0.97	-0.04	0.94	0.05
	Np	0.96	-0.13	0.91	0.05
	El	0.89	0.33	0.74	0.61
	Cont	0.01	0.99	0.02	0.99
% variance explained		66.45	27.44	63.24	26.85
B. viridis					
	Ri	0.92		0.90	
	Np	0.88		0.89	
	El	0.87		0.73	
	Cont	0.45		0.71	
% variance explained		64.51		66.25	

Note: All factors were standardized prior to analysis. Ri = habitat richness, Np = number of patches, El = edge length, Cont = contagion-index. For *B. viridis* only the first component was extracted.

Appendix C. Candidate models used for predicting home-range size (log-HRS).

Mod no.	Factors		Explanation - key features	Reference
1	Wood	+ N + Sex	partial habitat structure (area of large wood deposits, which is the preferred habitat)	Pasinelli 2000, McLoughlin et al. 2003, Buner et al. 2005
2	Wood + Ri	+ N + Sex	total habitat structure (area of large wood deposits plus habitat richness)	Kie et al. 2002
3	Wood + Ri + T	+ N + Sex	total habitat structure and habitat temperature	Schwarzkopf and Alford 1996, Seebacher and Alford 2002
4	Prey	+ N + Sex	prey density	McNab 1963, Ebersole 1980
5	Prey + T	+ N + Sex	prey density and habitat temperature	Pereira et al. 2002
6	Prey + T + Ri	+ N + Sex	prey density, habitat temperature and habitat structure	Tufto et al. 1996, Lombardi et al. 2007
7	Prey + Co	+ N + Sex	prey density and competition	Hixon 1980
8	Prey + Co + Ri	+ N + Sex	prey density, competition and habitat structure	Burt 1943, Kleeberger 1985, Smyers et al. 2002
9	M	+ N + Sex	body mass not important	Relyea et al. 2000, Said and Servanty 2005
10	N	+ Sex	number of locations (sampling bias)	Börger et al. 2006*a*, Fieberg 2007
11	A	+ N + Sex	differences in quality among animals not important	Steury and Murray 2003

Note: See Table 1 for abbreviations of factors. The number of locations (N) was used as a covariate in every model (except model 10) to correct for sampling bias. Similarly, sex was used in every model to correct for its potential effect on home-range size.

Eleven candidate models were formulated based on previous studies and our present field observation to address the three hypotheses. Models 1-3 hypothesized that habitat factors (habitat richness, area of large wood deposits, home-range temperature) determine home-range size (hypothesis 1). Model 7 hypothesized that biotic factors (prey density, competition) determine home-range size. Models 5, 6 and 8 hypothesized both habitat and biotic factors to determine home-range size (hypothesis 2). Models 9-11 hypothesized that individual factors (body mass, sex, animal identity) determined home-range size (hypothesis 3).

Models 1-2 were nested within model 3 to evaluate the relative contribution of the preferred habitat type (area of large wood deposits) (see Appendix C), habitat richness, and home-range temperature to variance in home-range size. Each model, except model 10, included the number of locations to correct for sampling bias. We preferred to use the number of locations as a covariate instead of estimating home-ranges with equal numbers of randomly selected locations, as proposed by Börger et al. (2006*a*) and Fieberg (2007). The former approach allowed us to quantify the separate effect of sampling bias. In each model, sex was used as a factor to correct for its potential effect on home range size. Emphasis was put on minimizing the set of factors and number of models to avoid bias in model selection. Interactions between factors were excluded because of the rather small sample size, and to avoid overfitted models.

For home-range calculation we used data of both years, taking individuals as sample units. For model selection we used data from 2006 because prey density was not sampled in 2005. Candidate models were fitted with general linear models (GLM, family=Gaussian, link=identity) in R version 2.4.0 (R Development Core Team (2005), separately per species and scale using the same sample size (Anderson and Burnham 2002). All factors were z-standardized prior to analysis. Home-range size was log-transformed to assure normally distributed residuals. One outlier (Cook's distance > 1) was removed.

Appendix D. Model selection results for predicting intraspecific variation in log-home-range size, sorted after differences between Akaike's small sample information criterion (ΔAICc), separately by species, the 50% core area, and the 95% home-range.

Model no.	Models	R^2	*K*	*LL*	AICc	ΔAICc	ωi	ER
Bufo bufo, 50% core area (*n* = 23)								
6	**Prey+Ri+T**	0.992	7	45.9	-70.3	0.0	**0.585**	1
5	**Prey+T**	0.990	6	43.1	-69.0	1.3	**0.312**	2
4	**Prey**	0.987	5	40.0	-66.4	3.9	**0.085**	7
7	Prey+Co	0.987	6	40.0	-62.7	7.6	0.013	44
8	Prey+Ri+Co	0.989	7	41.1	-60.8	9.5	0.005	117
3	Wood+Ri+T	0.935	7	21.1	-20.7	49.6	0.000	6.E+10
2	Wood+Ri	0.916	6	18.2	-19.2	51.1	0.000	1.E+11
1	Wood	0.615	5	0.7	12.1	82.4	0.000	8.E+17
10	N	0.143	4	-8.5	27.2	97.5	0.000	1.E+21
9	M	0.112	5	-8.1	30.2	100.5	0.000	7.E+21
11	A	0.150	5	-8.4	30.3	100.6	0.000	7.E+21
Bufo bufo, 95% home-range (*n* = 22)								
4	**Prey**	0.988	6	31.8	-63.4	0.0	**0.599**	1
5	**Prey+T**	0.989	7	33.1	-60.8	1.8	**0.245**	2
7	**Prey+Co**	0.984	5	28.3	-60.4	3.1	**0.125**	5
6	Prey+Ri+T	0.984	6	28.7	-56.7	6.2	0.027	22
8	Prey+Ri+Co	0.985	7	29.0	-56.2	10.0	0.004	147
2	Wood+Ri	0.769	6	-0.7	12.8	65.1	0.000	1.E+14
3	Wood+Ri+T	0.791	7	0.4	14.9	67.3	0.000	4.E+14
1	Wood	0.635	5	-5.7	21.3	71.3	0.000	3.E+15
9	M	0.352	5	-12.1	33.3	83.9	0.000	2.E+18
11	A	0.252	5	-11.7	34.0	84.1	0.000	2.E+18
10	N	0.211	4	-14.2	34.5	84.8	0.000	3.E+18
Bufo viridis, 50% core area (*n* = 24)								
1	**Wood**	0.916	5	4.5	4.3	0.0	**0.798**	1
2	**Wood+Ri**	0.918	6	4.7	7.5	3.2	**0.162**	5
3	Wood+Ri+T	0.922	7	5.4	10.2	6.0	0.041	20
4	Prey	0.783	5	-6.9	27.1	22.9	0.000	9.E+04
5	Prey+T	0.783	6	-6.9	30.7	26.4	0.000	6.E+05
7	Prey+Co	0.783	6	-6.9	30.7	26.5	0.000	6.E+05
6	Prey+Ri+T	0.794	7	-6.3	33.6	29.3	0.000	2.E+06
8	Prey+Ri+Co	0.792	7	-6.4	33.8	29.5	0.000	3.E+06
10	N	0.126	4	-23.6	57.3	53.1	0.000	3.E+11
9	M	0.166	5	-22.1	57.6	53.4	0.000	4.E+11
11	A	0.129	5	-23.6	60.5	56.2	0.000	2.E+12

<u>*Bufo viridis*, 95% home-range (*n* = 28)</u>

2	**Wood+Ri**	0.784	7	2.8	-4.9	0.0	**0.400**	1
3	**Wood+Ri+T**	0.780	7	3.0	-5.2	0.6	**0.290**	1
6	**Prey+Ri+T**	0.716	5	1.9	-8.9	1.2	**0.214**	2
8	**Prey+Ri+Co**	0.719	6	1.8	-8.7	4.1	**0.051**	8
1	Wood	0.717	6	-3.7	-8.9	4.4	0.045	9
4	Prey	0.593	6	-5.2	-14.1	14.9	0.000	1741
5	Prey+T	0.511	5	-3.7	-16.8	17.1	0.000	5050
7	Prey+Co	0.610	7	-4.7	-13.5	17.2	0.000	5343
10	N	0.273	5	-14.4	-19.4	22.7	0.000	9.E+04
9	M	0.332	4	-13.8	-21.3	23.1	0.000	1.E+05
11	A	0.334	5	-14.0	-21.3	26.0	0.000	4.E+05

Note: See Table 1 for abbreviations of factors. The top ranked model with ΔAICc = 0 best approximates the data and models with ΔAICc ≤ 2 are considered to receive substantial support from the data. The number of animals (*n*), the coefficient of determination (R^2), number of factors (*K*), log-likelihood (*LL*), model weights (ωi) and evidence ratios (ER) are given. When one model receives ωi ≥ 0.9 there is no model selection uncertainty apparent. ER are the ratio of model weights of a particular model in relation to the top ranked model. Models in bold face (confidence set: sum of ωi ≥ 0.9) were used for model averaging.

Appendix E. Model-averaged factors of intraspecific variation in home-range size for both species, the 50% core area and the 95% home-range.

	50% core area					95% home-range				
Factors	Beta	SE	CV	LCI	UCI	Beta	SE	CV	LCI	UCI
Bufo b. spinosus										
A										
Co						-0.025	0.019	0.764	-0.063	0.012
Wood										
N	0.012	0.026	2.132	-0.040	0.064	-0.003	0.047	14.450	-0.096	0.089
Prey	**0.333**	**0.048**	**0.145**	**0.236**	**0.430**	**0.461**	**0.056**	**0.121**	**0.352**	**0.571**
Ri	**0.059**	**0.028**	**0.468**	**0.004**	**0.114**	-0.040	0.028	0.704	-0.094	0.015
Sex	0.039	0.065	1.676	-0.092	0.169	0.008	0.105	12.392	-0.197	0.214
T	0.090	0.063	0.696	-0.035	0.215					
M										
B. viridis										
A										
Co						0.032	0.180	5.641	-0.321	0.384
Wood	**0.705**	**0.125**	**0.177**	**0.456**	**0.954**					
N	0.146	0.137	0.942	-0.129	0.420	0.174	0.284	1.629	-0.382	0.730
Prey						0.429	0.289	0.673	-0.137	0.996
Ri	0.038	0.065	1.739	-0.093	0.168	0.214	0.160	0.744	-0.098	0.527
Sex	-0.110	0.204	1.851	-0.519	0.298	-0.050	0.582	11.590	-1.192	1.091
T						-0.057	0.069	1.202	-0.192	0.078
M										

Note: See Table 1 for abbreviations of factors. All factors were standardized prior to analysis. Unconditional effect size (Beta: slopes of factors in general linear models) with standard error (SE), coefficient of variation ($|CV|$ = SE / Beta), lower (LCI) and upper (UCI) confidence interval (Beta ± 2 SE). Betas, SE and CV are based on a confidence model-set (summarized weights ≥ 0.90). Factors without values were not included in the model set used for model-averaging. Factors that did not include zero in confidence intervals are considered as important (bold).

Hypothesis 1: Habitat factors control the size of 50% core areas

For *B. b. spinosus*, the three top-ranked models that were best supported by the data included the factors habitat richness, home-range temperature, and prey density (Appendix D). The top-ranked model (no. 6) was twice as well supported as the second ranked model (no. 5), and seven times better supported than the third-ranked model (no. 4) (see evidence ratios, Appendix D). The effect of prey density on its 50% core area was almost six times larger than was the effect of habitat richness (Appendix E). For *B. b. spinosus*, hypothesis 1 was partly supported, as both habitat factors (habitat richness) and biotic factors (prey density) determined the 50% core area. For *B. viridis*, the best selected model (no. 1) ($\omega i > 0.798$) contained the factor area of large wood deposits (Appendix D), which solely determined its 50% core area (Appendix E), partly supporting hypothesis 1.

For both species, the factor home-range temperature was poorly supported (confidence intervals included zero) (Appendix E), contrasting with our hypothesis.

Hypothesis 2: Biotic factors control the size of 95% home-ranges

For *B. b. spinosus*, although the three top-ranked models (nos. 4, 5, and 7) (sum of $\omega i > 0.9$) contained the factors home-range temperature, prey density, and competition (Appendix D), prey density alone determined the 95% home-range (Appendix E), partly supporting hypothesis 2. In contrast, for *B. viridis*, the three top-ranked models (nos. 2, 3, and 6) contained habitat richness, area of large wood deposits, home-range temperature and prey density ($\omega i > 0.9$) (Appendix D). For *B. viridis*, hypothesis 2 was partly supported as both habitat factors (habitat richness) and biotic factors (prey density) predicted the size of 95% home-ranges (Appendix E), though confidence intervals included zero. Competition poorly explained the variation in 95% home-ranges of both species (confidence intervals included zero) (Appendix E), contrasting with our hypothesis.

Hypothesis 3: The effects of individual factors are outweighed by the effects of habitat and biotic factors.

All individual factors (models 9-11) poorly predicted variation in the size of 50% core areas and 95% home-ranges (confidence intervals included zero) (Appendix E), fully supporting hypothesis 3. Results were consistent when using the number of weeks instead the number of locations to correct for sampling bias (Appendix F).

In summary, the most important home-range-size determinants were prey density, habitat structure (habitat richness and area of large wood deposits), and temperature.

Appendix F. Model-averaged factors of intraspecific variation in home-range size for both species, the 50% core area and the 95% home-range.

	95% home-range									
	Bufo b. spinosus					*B. viridis*				
Factors	Beta	SE	|CV|	LCI	UCI	Beta	SE	|CV|	LCI	UCI
A										
Co	-0.026	0.019	0.720	-0.064	0.011	-0.007	0.089	12.535	-0.181	0.167
Wood										
Week	0.013	0.050	3.862	-0.086	0.112	0.175	0.211	1.210	-0.240	0.590
Prey	**0.453**	**0.058**	**0.129**	**0.338**	**0.568**	**0.414**	**0.203**	**0.491**	**0.015**	**0.814**
Ri	-0.032	0.027	0.834	-0.086	0.020	0.247	0.155	0.628	-0.057	0.551
Sex	-0.001	0.102	174.325	-0.202	0.201	-0.079	0.434	5.427	-0.930	0.770
T						-0.115	0.068	0.592	-0.250	0.018
M										

Note: Here, the number of weeks (Week) was used to correct for sampling bias while in Appendix E the number of locations collected was used to correct for sampling bias. See Table 1 for abbreviations of other factors. All factors were standardized prior to analysis. Unconditional effect size (Beta: slopes of factors in general linear models) with standard error (SE), coefficient of variation (│CV│ = SE / Beta), lower (LCI) and upper (UCI) confidence interval (Beta ± 2 SE). Betas, SE and CV are based on a confidence model-set (summarized weights ≥ 0.90). Factors without values were not included in the model set used for model-averaging. Factors that did not include zero in confidence intervals are considered as important (bold).

Appendix G. Correlation matrix of factors used in candidate models for predicting log-home-range size, separated by species, the 50% core area, and the 95% home-range.

Factors	*n*	logHRS	Ri	Wood	Prey	Co	M	T	N	Week
Bufo bufo, 50% core area										
logHRS	54	1.000	0.938	0.710	0.993	-0.331	-0.047	0.432	0.345	0.272
Ri	54		1.000	0.708	0.942	-0.259	-0.068	0.262	0.181	0.141
Wood	54			1.000	0.777	-0.167	-0.113	0.180	0.016	-0.084
Prey	23				1.000	-0.343	-0.061	0.380	0.300	0.243
Co	54					1.000	-0.198	0.017	0.114	-0.007
M	51						1.000	-0.450	0.169	0.101
T	54							1.000	0.375	0.238
N	54								1.000	0.818
Week	54									1.000
Bufo bufo, 95% home-range										
logHRS	54	1.000	0.760	0.686	0.992	-0.215	-0.265	0.549	0.261	0.408
Ri	54		1.000	0.611	0.774	-0.279	-0.101	0.306	0.081	0.216
Wood	54			1.000	0.705	-0.120	-0.265	0.274	0.011	0.163
Prey	22				1.000	-0.124	-0.284	0.560	0.259	0.414
Co	54					1.000	0.094	-0.119	0.093	0.037
M	51						1.000	-0.539	0.232	0.179
T	54							1.000	0.141	0.323
N	54								1.000	0.802
Week	54									1.000
B. viridis, 50% core area										
logHRS	59	1.000	0.639	0.940	0.839	-0.022	0.103	0.556	0.182	0.159
Ri	59		1.000	0.614	0.596	-0.135	0.402	0.574	0.096	-0.159
Wood	59			1.000	0.834	-0.127	0.181	0.579	0.045	0.088
Prey	26				1.000	0.015	0.314	0.557	0.149	0.176
Co	59					1.000	-0.213	-0.166	-0.318	0.106
M	57						1.000	0.314	-0.136	0.142
T	59							1.000	0.074	0.027
N	59								1.000	0.490
Week	59									1.000
B. viridis, 95% home-range										
logHRS	59	1.000	0.583	0.536	0.851	-0.005	0.003	0.239	0.538	0.343
Ri	59		1.000	0.383	0.427	-0.438	-0.048	0.552	0.287	0.138
Wood	59			1.000	0.698	0.094	0.127	0.380	0.169	0.185
Prey	29				1.000	0.027	0.037	0.351	0.379	0.248
Co	59					1.000	0.087	-0.308	-0.126	0.407

M	57	1.000	-0.004	0.148	0.234
T	59		1.000	0.140	0.064
N	59			1.000	0.609
Week	59				1.000

Note: See Table 1 for abbreviations of factors. All factors were standardized prior to calculating Pearson coefficients. *n* = number of animals.

Appendix H. Distribution of locations, classified as "resting" or "foraging", in 50% core areas and 95% home-ranges. *n* = number of locations.

	Bufo b. spinosus				*B. viridis*			
			n in % of total *n* in				*n* in % of total *n* in	
	n	%	core area	home-range	*n*	%	core area	home-range
Seen	1116	35.1	13.7	31.7	1152	45.1	17.4	42.7
Not seen	2063	64.9	36.7	61.8	1404	54.9	38.5	54.3
Total	3179	100.0	50.3	93.6	2556	100.0	55.9	97.0
Seen at day	406	36.4	16.2	33.2	374	32.5	19.4	31.7
Seen at night	710	63.6	22.7	57.3	776	67.5	19.1	63.0
Total	1116	100.0	38.9	90.4	1150	100.0	38.5	94.8
Not seen at day	1329	64.4	37.0	61.2	985	70.3	49.8	69.5
Not seen at night	734	35.6	19.5	34.0	417	29.7	20.3	29.4
Total	2063	100.0	56.5	95.2	1402	100.0	70.0	98.9
Seen moving	156	19.6	5.4	17.2	342	43.1	9.3	40.2
Seen sitting	639	80.4	31.9	72.5	451	56.9	27.7	55.0
Total	795	100.0	37.4	89.7	793	100.0	37.1	95.2
Seen moving at day	23	14.7	6.4	14.1	13	3.8	1.5	3.8
Seen moving at night	133	85.3	21.2	73.7	329	96.2	20.2	89.5
Total	156	100.0	27.6	87.8	342	100.0	21.6	93.3
Seen sitting at day	274	42.9	16.7	38.2	242	53.7	33.0	52.5
Seen sitting at night	365	57.1	23.0	52.0	209	46.3	15.7	44.1
Total	639	100.0	39.7	90.1	451	100.0	48.8	96.7

CHAPTER 3

Differential resource selection within shared habitat types across spatial scales in sympatric toads

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Abstract. Differential habitat selection is a central component in the evolution of species, but has proven difficult to measure empirically. We quantified the selection of terrestrial summer habitats in a complex floodplain by two sympatric amphibians (*Bufo b. spinosus* and *B. viridis*) as a function of habitat type, a biotic (prey density) and an abiotic resource (temperature). We applied a novel resource selection model, accounting for differences among individuals, at three spatial scales: a) home-range placement within the floodplain, b) space use within 95% home-ranges, and c) space use within 50% core areas.

We hypothesized that home-range placement is determined by both prey density and temperature because they are essential factors in summer for both species (H1). Summer home-ranges integrate spacious foraging and confined resting behavior. We therefore hypothesized that habitat use within

95% of home-ranges is determined by prey density (H2) and within 50% of core areas by temperature (H3). Last, we predicted that the two species exhibit differential resource selection for shared habitat types across spatial scales (H4) because this would facilitate co-existence.

The most complex candidate model which included habitat type, prey density, temperature, and all interactions best explained habitat selection of both species across all scales. Hence, H1 was fully supported whereas H2 and H3 were partially supported. This result suggests that amphibians perceive resource gradients at all spatial scales, and that all spatial scales are important for regulating foraging behavior and thermoregulation.

Both species largely preferred the same habitat types. The same habitat types, however, were used differently in relation to resources across the three spatial scales, supporting hypothesis 4. Niche differentiation through differential resource selection within shared habitat types across spatial scales may therefore facilitate the co-existence of the two species in terrestrial summer habitat. We graphically explored the interactive effects of habitat type, prey density and temperature by applying predictions and found that home-range placement was determined by the availability of habitat types rather than resources. This was puzzling as we found that prey density was lower and temperature higher outside home-ranges than within home-ranges. Within 95% home-ranges and 50% core areas, space use was strongly dependent on resources. These patterns indicate that home-range placement can be influenced by intrinsic factors such as genetic differences between species, whereas space use within home-ranges is determined by resource gradients.

Introduction

Co-existence of species can arise through avoidance of competition (Gause 1934, Hardin 1960). Competition in turn may be avoided through the spatiotemporal partitioning of habitats and resources (Hairston 1951, Whittaker 1967, Pianka 1969, Diamond 1973). In this context, differential habitat selection is a key process that stabilizes co-existence of species (MacArthur and Levins 1967, Rosenzweig 1991, Chesson 2000). The detection of differential habitat selection requires information across the spatial and temporal scales at which animals operate (Hutchinson 1957, Wiens 1973). This information is methodically difficult to get and may explain why the combined effects of various resources on habitat selection of sympatric species have been rarely studied empirically (but see Anthony and Smith 1977, Bourget et al. 2007, Gilbert et al. 2008). To shed more light on the potential mechanisms for co-existence we need to explore the interplay of various resources and their gradients on habitat selection of sympatric species across multiple spatial scales.

Habitat selection is a spatially hierarchical process in which animals first place home-ranges within a larger area and subsequently use patches within home-ranges (Johnson 1980). Home-range placement is most important, as it determines the number of patches for exploitation by animals. Home-range placement is usually done quickly and is based on general features of the environment (Lack 1940, MacArthur et al. 1966, Cody 1981). Subsequent habitat selection within home-ranges, where the environment is best perceived by the animal, may include the availability of prey and refuge. Hierarchical habitat selection is therefore thought to be a solution to cope with spatiotemporal variation in resource availability (Levins 1968, Orians and Wittenberger 1991). This idea has found empirical support in a few studies (Nikula et al. 2004, Pinaud and Weimerskirch 2005, Beasley et al. 2007).

The hierarchical nature of habitat selection suggests that space use within home ranges is conditional on home-range placement. Home-range placement is therefore proposed to be controlled by the most limiting resources, whereas space use at smaller spatial scales is governed by less limiting resources (Rettie and Messier 2000). Exploring habitat selection across spatial scales can provide insight on the importance of resources as well as on how animals perceive variation in resource availability.

Habitat selection is increasingly quantified using resource selection models (Manly et al. 2002). Resource selection models usually ignore variation in habitat selection among individuals (but see Gillies et al. 2006, Thomas et al. 2006, Hebblewhite and Merrill 2008). However, individuals may differ in habitat selection due to variation in physiological state or tolerance to limiting resources. We therefore applied a novel resource selection model, accounting for differences among individuals, to avoid bias that may result from ignoring inter-individual variation.

In this study, we quantified the selection of terrestrial summer habitats of two pond-breeding amphibians (*Bufo b. spinosus, B. viridis*). These species co-occur within the active tract of a naturally dynamic floodplain (Tockner et al. 2006). We studied the terrestrial summer period because of its importance for population viability (Schmidt et al. 2005, Rittenhouse and Semlitsch 2007). The most important resources in summer for these amphibians are food and shelter. Abundant food is required to build up fat reserves for physiological maintenance and future reproduction (Waelti and Reyer 2007), while cool habitats are refugia for animals from desiccation

(Schwarzkopf and Alford 1996, Seebacher and Alford 2002). The study floodplain is characterized by summer droughts and a spatially complex habitat mosaic (Ward et al. 1999, Tockner et al. 2003). This study system provides the essential characteristics to detect habitat selection: i.e., a strong selection pressure and high variation in resource availability.

Our main goal was to quantify habitat selection as a function of habitat type and resources (prey, temperature) at three spatially hierarchical scales that were expected to integrate different behaviors (Marzluff et al. 2001): a) home-range placement within the floodplain, b) space use within 95% home-ranges, and c) space use within 50% core areas. Four hypotheses were tested:

1. Prey density and temperature determine home-range placement within the floodplain because they are essential factors in summer for both species.

2. Prey density determines space use within 95% home-ranges, which are assumed to mainly integrate spacious foraging behavior for both species.

3. Temperature determines space use within 50% core areas, which is assumed to mainly integrate confined resting behavior for both species.

4. Species select shared habitat types differently in relation to prey density and temperature across the three spatial scales examined. Such differential use of floodplain habitat across these spatial scales would allow the two species to coexist.

Methods

Study site

The study was conducted from mid-June through September in 2005 and 2006 on the 7th order Tagliamento River in northeastern Italy (46°N, 12°30'E). The Tagliamento (catchment area: 2580 km^2) originates at 1000 m asl in the southern fringe of the European Alps and flows almost unimpeded by dams for 172 km to the Adriatic Sea. The river retains its essentially pristine morphological and hydrological characteristics. The main study area was the active tract (1.6 km^2) of an island-braided floodplain complex (river-km 79.8 -80.8; 135 m asl). This reach contains a spatially complex and temporally dynamic habitat mosaic embedded into an extensive matrix of exposed riverine sediments (Petts et al. 2000) (chapter 1, Fig. 1). The 800 m wide active tract is fringed by riparian forest (right bank). The steep hillslope of Monte Ragogna borders the left bank of the floodplain. Further detailed information on the Tagliamento catchment and the main study area can be found elsewhere (Ward et al. 1999, Arscott et al. 2002, Tockner et al. 2003).

Study species

Bufo b. spinosus (common toad) is a generalist species with a Palaearctic distribution. It is associated with densely vegetated habitats of old succession stages. *B. viridis* (green toad) is a pioneer species, characteristic of open habitats such as hot steppe (Giacoma and Castellano 2006).

Habitat mapping

In 2005 and 2006, the entire study area was mapped in detail at base flow (about 20 $m^3 s^{-1}$) using a differential GPS (Trimble GeoXT) (Fig. 1). GPS data were processed using ArcView GIS 9.0 (ESRI). We discriminated six habitat types that were mutually exclusive: exposed gravel sediments (70.3 ha; average values for both years), water (13.5 ha), established islands (8.3 ha), edge of established islands (6.4 ha), dense pioneer vegetation (3.9 ha), and area of large wood deposits (1.2 ha) (Table 1). The habitat type water was excluded for analysis because it was used by only a few toads. The edge of established islands was included because edge habitat provides complementary food resources (Morris 1987).

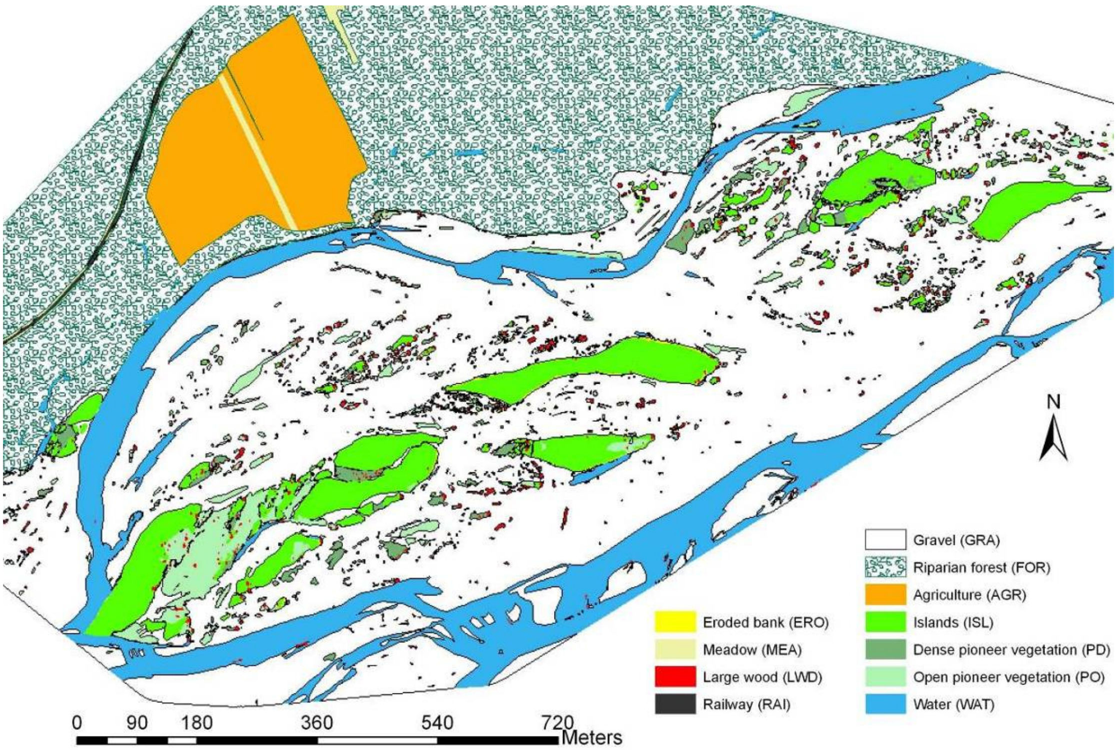

Figure 1. GIS-map of the study site.

Table 1. Mean spatial extent (ha, % of total floodplain area) of all habitat types in 2005 and 2006, and the distribution of locations in 95% home-ranges (*n*, % of total) for each species. The relative intensity of habitat use is given by the proportions of locations (U) over the proportion of available habitat (A). U/A < 1 denotes habitat types that were less used compared to their availability.

		Availability (A=%area)		Used (U=%locations) *Bufo b. spinosus*			*B. viridis*			Mean maximum temperature[§] [°C]		Log-prey density[§§] [m^2]	
Code	Habitat type	[ha]	%	*n*	%	U/A	*n*	%	U/A	mean	SD	mean	SD
GRA	Exposed gravel sediments	70.32	67.6	701	23.3	0.34	1131	46.2	0.68	43.3	3.1	0.199	0.367
LWD	Large wood deposits[*]	1.26	1.2	589	19.6	16.12	850	34.8	28.59	27.2	2.2	0.182	0.374
PD	Dense pioneer vegetation[†]	3.98	3.8	248	8.3	2.15	227	9.3	2.42	35.4	2.8	0.440	0.402
ISL	Established islands[‡]	8.32	8.0	693	23.1	2.88	27	1.1	0.14	33.5	2.8	0.724	0.360
ISLE	Island edge[**]	6.48	6.2	753	25.0	4.02	205	8.4	1.34	34.8	4.2	0.171	0.308
WAT	Water[††]	13.59	13.1	22	0.7	0.06	6	0.2	0.02				
	Sum	103.97	100.0	3006	100.0		2446	100.0					

[*] minimum size of 0.5 m^2

[†] vegetation cover >50%; minimum size of 1 m^2

[‡] island with wooded perennial vegetation higher than 2 m, surrounded by water or exposed gravel

[**] buffer of 10 m, centered along the shelter rich border of established islands with slopes between 45 and 90°

[††] not considered for analysis because of its availability only to a few animals

[§] based on 124 temperature loggers that were distributed proportionally over the habitat types. Mean maximum temperature was calculated using hourly measures from 8 a.m to 8. p.m.

[§§] based on 100 pitfall traps that were distributed proportionally over the habitat types. Pitfalls were sampled at three occasions in summer.

Determinants of habitat selection

Three explanatory factors were used for modelling the selection of 1-m^2 patches: log-prey density (P), temperature (T), and habitat type (H), which was expressed by five binary indicator factors. A single habitat type (Table 1) was assigned per patch. We defined habitat patches as grid cells of 1-m^2 because animals rarely used smaller patches of the most preferred habitat type (large wood deposits).

Temperature and prey density were calculated as follows: Temperature loggers (Thermochron ibuttons DS1921G, 0.5°C resolution, ±1°C accuracy from -30°C to 70°C; 2005: 67 loggers; 2006: 57 loggers) were randomly distributed in proportion to the area cover of individual habitat types. Temperature was logged at the sediment surface at hourly intervals. Mean maximum day temperature, measured within each habitat type, was assigned to each corresponding habitat patch. Temperature values of habitat patches were linearly weighted according to temperature gradients from island cores to the island edge and from island edges to exposed gravel sediments.

Prey density was quantified in 2006 by setting up 100 pitfall traps (diameter 9 cm, depth 12 cm, volume 0.5 l) randomly along three transects perpendicular to the river corridor. The pitfalls were sampled three times in 2006 (21/22 July, 8/9 August, 7/8 September), and were opened (set) at twilight (8:00-9:30 p.m.) and closed at sunrise (5:00-7:00 a.m.). Assuming that all the contents of the pitfall traps were consumable, average prey density within the active tract was determined per sampling date by applying an inverse distance-weighted interpolation method in ArcGIS 9.0 (ESRI), using log-transformed prey densities. The three interpolations were averaged, and the fit of the averaged cross-validated interpolation was moderate (R^2 = 0.466).

Radio telemetry

Adult toads were caught during random searches at night time and marked with radio transmitters LT2-351 (2g) or LT2-392 (5g) (Titley Electronics Ltd, Ballina, Australia). The radio transmitters were tightly fitted with an aluminium beaded-chain belt (Ball Chain Manufacturing Co., New York, USA) around the waist (Rathbun and Murphey 1996, Indermaur et al. 2008) (chapter 1, Fig. 2). The mass of the transmitter, including the belt, did not exceed 10% of the body mass of toads (mean ± SD: *B. b. spinosus*: 4.32 ± 1.51 %; *B. viridis*: 6.86 ± 0.94 %) as recommended by Richards et al. (1994). Neither transmitter mass nor duration of the tracking period negatively affected changes in toad body mass (Indermaur et al. 2008).

Australis 26k scanning receivers and hand-held three-element Yagi antennas (Model AY/C, Yagi collapsible) were used (Titley Electronics Ltd, Ballina, Australia) for tracking toads. We followed 56 radio-tagged *B. b. spinosus* and 59 *B. viridis* between one and three months (mean range: *B. b. spinosus*: 44.5 d, 13.4-99.5 d; *B. viridis*: 33.1 d, 13.5-71 d). The exact position of each toad was recorded six days a week, once at day and once at night, using a dGPS (average tracking resolution: 1 m). Two observers simultaneously located toads in different parts of the study area, randomly varying the tracking time and the sequence of tracked animals. See chapter 1, Fig. 3, Appendix A for further detail on tracking methods.

Estimation of home-ranges

For home-range estimation, 3079 locations of *B. b. spinosus* and 2545 locations of *B. viridis* were used, from which we derived a mean of 55 ± 27.6 (mean ± SD) locations for each individual of *B. b. spinosus* and 43 ± 16 locations of each individual of *B. viridis*. Fixed kernel home-ranges were calculated with software "Ranges 7" (grid: 160 x 160 cells, cell size: 1 m^2) using either 50% or 95% of the locations (Kenward and Hodder 1996), and by applying a least-squares cross-validate smoothing factor (h = 0.3). For home-range distribution, see chapter 2, Fig. 2. The 50% of core area was determined by applying a regression of probability of use against the proportion of total area (Clutton-Brock et al. 1982, Powell 2000) (see chapter 2, Fig. 1).

Statistical analysis

We quantified hierarchical habitat selection (Johnson 1980), expressed at three spatial scales: home-range placement within the floodplain, space use within 95% home-ranges, and space use within 50% core areas. In 95% home-ranges and 50% core areas, toads spent about 95% or 50% of their time, respectively. The 95% home-range was about 10 times larger than the 50% core area (mean ± SD: *B. b. spinosus*: 50% core area: 48 ± 78 m^2, 95% home-range: 570 ± 872 m^2; *B. viridis*: 50% core area: 295 ± 806 m^2, 95% home-range: 2456 ± 3946 m^2). The 95% home-range is therefore expected to mainly integrate spacious foraging behavior, while the 50% core area is expected to integrate confined resting behavior.

For the analysis, we used radio locations of 27 individuals of *B. b. spinosus* (BB) and 32 individuals of *B. viridis* (BV) that were tracked in 2006 (home-range placement: BB: n = 1354, BV: n = 1379; space use within 95% home-ranges: BB: n = 1229, BV: n = 1347; space use within 50% core areas: BB: n = 665, BV, n = 793). Radio locations collected in 2005 were excluded because prey density was not sampled then.

We quantified habitat use (number of selected 1-m^2 patches) and habitat availability (number of presumably avoided 1-m^2 patches) separately per individual, species and scale. Data for resources (prey density, temperature) were available at the patch level. The number of used patches per individual was given by the number of patches containing a location.

The number of available habitat patches per individual was chosen in proportion to used patches to reduce potential bias in results that might come from asymmetry in the number used and available patches (Johnson et al. 2006). When individuals place home-ranges within the floodplain, the entire floodplain habitat is virtually available for selection. Within home-ranges, there is much less habitat available to individuals, compared to the entire floodplain. Hence, we varied habitat availability across scales: i) for home-range placement, the number of available patches was randomly selected per animal from 552 822 available patches within the floodplain; ii) for space use within 95% home-ranges and iii) within 50% core areas, we randomly chose available patches per animal within its 95% home-range or within its 50% core area. As few animals were shown to cross the entire study area within a single night (L. Indermaur, *unpublished data*), we consider distant patches within the entire study area available to animals.

We used a hierarchical logistic-regression model within the Bayesian framework for modelling habitat selection by toads. The dependent variable (y) was 0 when the corresponding patch was not visited and 1 when the patch was used by toads. Traditional habitat selection studies have analysed these kinds of data using a logistic regression model applied for each individual separately. Combining all individuals and applying this model would be wrong because the unit of the analysis must be the individual and not the single observation. This problem is circumvented in a hierarchical model. Loosely spoken, the hierarchical logistic regression model fits a curve for each individual, and then regards the curves of each individual as a further sample from which the overall relationship is estimated. Thus, for each individual j (j = 1…J) and each observation i (i = 1…I) the dependent variable $y_{i,j}$ follows a Bernoulli distribution

$$y_{i,j} \sim \mathrm{Bern}\left(\mu_{i,j}\right)$$

The expected value $\mu_{i,j}$ is modelled by factors describing the patch using the logit link function in various combinations (Table 2). For simplicity, we present a model including the main effects only (Table 2, model 10)

$$\mathrm{logit}\left(\mu_{i,j}\right) = \alpha_j P_{i,j} + \beta_j T_{i,j} + \gamma_{j,h} H_{i,j}$$

where $P_{i,j}$ is prey density, $T_{i,j}$ is temperature, and $H_{i,j}$ is habitat type (5 levels: exposed gravel sediments, large wood deposits, dense pioneer vegetation, established islands, edge of established islands) for individual j at observation i. Because the habitat is categorical, there are different parameters for each habitat type. The individual slope parameters are then modelled with a normal distribution to estimate the population mean and variance.

$$\alpha_j \sim \mathrm{N}(\overline{\alpha}, \sigma_\alpha^2)$$

$$\beta_j \sim \mathrm{N}(\overline{\beta}, \sigma_\beta^2)$$

$$\gamma_{j,h} \sim \mathrm{N}(\overline{\gamma}_h, \sigma_{\gamma,h}^2)$$

We were particularly interested in estimating the population slope parameters ($\overline{\alpha}, \overline{\beta}, \overline{\gamma}_h$). The variability ($\sigma_\alpha^2, \sigma_\beta^2, \sigma_{\gamma,h}^2$) is a measure of how strongly the individuals differed regarding the preference for specific habitat characteristics. For a more detailed description of hierarchical models we refer readers to Gelman and Hill (2007). We specified non-informative priors for all parameters to be estimated. We used N(0, 0.001) priors for the slope parameters and, following Gelman (2005), uniform priors U(0,100) for the variance parameters.

To calculate the posterior distributions of the parameters of interest, we used Markov Chain Monte Carlo simulations implemented in program WinBUGS (Lunn et al. 2000) that we executed from R (R Development Core Team 2005) with the package R2WinBUGS (Sturtz et al. 2005). We ran 3 independent chains and checked the convergence using the Brooks – Rubin – Gelman diagnostic (Brooks and Gelman 1998). Convergence usually was obtained quickly. For each candidate model, we ran 3 chains with 80 000 iterations, discarded the first 25 000 iterations and saved every 10th sample. The explanatory factors were all standardized (mean = 0, sd = 1) prior to analysis.

Model selection

We asked whether habitat selection is determined by the separate or the combined effects of the main factors prey density, temperature, and habitat type (Hypotheses 1-3). We formulated a set of 17 candidate models (Table 2), and fitted each with the hierarchical logistic regression described above, separately by species and scale. Model 1 was the most complex model, including all possible interactions among main factors. The simplest models included single main factors (Models 13, 16, 17).

Table 2. Candidate models used to evaluate the best model for predicting habitat selection. P=Log-prey density, T=Temperature, H=Habitat type (5 levels).

Model No.	Covariates	Explanation
1*	P+T+H+(P*T)+(P*H)+(T*H)+(P*T*H)	Full model, all main factors and their interactions important
2*	P+T+H+(P*T)+(P*H)+(T*H)	Three-way interaction of prey density, temperature and habitat not important
3*	P+T+H+(P*T)+(P*H)	Interactions of prey density and temperature, and prey density with habitat important
4*	P+T+H+(P*T)+(T*H)	Interactions of prey density and temperature, and temperature with habitat important
5*	P+T+H+(P*H)	Interaction of prey density with habitat important
6*	P+T+H+(T*H)	Interaction of temperature with habitat important
7*	P+H+(P*H)	Interaction of prey density with habitat important, temperature not important
8*	T+H+(T*H)	Interaction of temperature with habitat important, prey density not important
9	P+T+H+(P*T)	Interaction of prey density and temperature important
10	P+T+H	All main factors without interactions important
11	P+H	Prey density and habitat important

12	T+H	Temperature and habitat important
13	H	Habitat important ("Nullmodel")
14	P+T+(P*T)	Habitat not important
15	P+T	Habitat not important
16	P	Habitat not important
17	T	Habitat not important

* due to increasing model complexity few parameters did not fully converge. Parameter estimates, however, were consistent when models were fitted repeatedly.

We use differences in the deviance information criterion scores (ΔDIC) and model weights to evaluate the support of models (Spiegelhalter et al. 2002). The ΔDIC is the difference of DIC between any model in the set to the best model. The smaller the ΔDIC the better the model is supported by the data. A single best model would have model weights ≥ 0.9, and if model weights were equally distributed across models, it would indicate all models to be equally supported.

Habitat- type specific predictions

We explored the potential for differential resource selection of shared habitat types by calculating predictions (Hypothesis 4). We estimated the selection probability for a habitat type across resource gradients. Predictions were based on the best model out of the model selection process. For simplicity we present the formula for the main effects here (but see Table 2).

$$P_H = \frac{\exp\left(\overline{\alpha} Pr_{pred} + \overline{\beta} T_{pred} + \overline{\gamma}_H\right)}{1 + \exp\left(\overline{\alpha} Pr_{pred} + \overline{\beta} T_{pred} + \overline{\gamma}_H\right)}$$

These predictions are probabilities (P_H) that the patch within habitat type H and with characteristics P_{pred} and T_{pred} was preferred ($P_H > 0.5$), avoided ($P_H < 0.5$), or randomly ($P_H = 0.5$) used. We calculated P_H for 14 temperature values spanning the range of observed values (T_{pred}: 20, 22, 24, ... 46°C), and three constant prey densities (P_{pred}): low (-0.1), intermediate (0.1), and high (0.7).

Results

Both species preferred the same habitat types within the floodplain, except that *B. viridis* avoided established islands (Table 1). Both species showed the strongest preference for large wood deposits. Established islands provided the highest prey density, followed by dense pioneer vegetation while large wood deposits provided lowest temperature, followed by established islands (Table 1).

Both species placed home-ranges in areas within the floodplain where prey density was slightly higher and temperature significantly lower than in avoided areas (mean log-prey density in selected/avoided areas: *B. b. spinosus*: 0.175 m^{-2}/0.145 m^{-2}, $t = 1.243$, $df = 27$, $p = 0.224$; *B. viridis*: 0.198 m^{-2}/0.148 m^{-2}, $t = 1.655$, $df = 31$, $p = 0.107$; mean temperature in selected/avoided areas: *B. b. spinosus*: 33.8 °C/42.8 °C, $t = 17.353$, $df = 29$, $p < 0.001$; *B. viridis*: 36.4 °C/42.6 °C, $t = 9.558$, $df = 37$, $p < 0.001$).

Prey density and temperature were uncorrelated at the level of home-range placement (*B. b. spinosus*: $r = -0.076$; *B. viridis*: $r = -0.088$), within 95% home-ranges (*B. b. spinosus*: $r = 0.141$; *B. viridis*: $r = 0.099$), and within 50% core areas (*B. b. spinosus*: $r = 0.23$; *B. viridis*: $r = -0.042$). Hence, prey density and temperature described different habitat characteristics.

Model selection

For *B. b. spinosus*, the most complex model (model 1, Table 2) was best selected across the three spatial scales (weights ≥ 0.8; Table 3). For *B. viridis*, models 1 and 2 predicted home-range placement equally well as indicated by the similar model weights. The difference between the models was a three-way interaction between habitat type, prey density, and temperature. Within 95% home-ranges of *B. viridis*, model 1 and 2 were best selected with model 1 being about 3.6 times better than model 2 (evidence ratio: 0.782 / 0.218 =3.6). Within 50% core areas of *B. viridis*, model 2 was selected best (Table 3).

Table 3. Model selection results for predicting habitat selection, sorted after the Deviance Information Criterion scores (ΔDIC), separately by species and scale. The best model (bold type) was used to predict habitat selection.

	B. b. spinosus					*B. viridis*				
Scale	Model No.	DEV	pD	ΔDIC	weights	Model No.	DEV	pD	ΔDIC	weights
Home-range placement within floodplain										
	1	236	58	0.0	0.975	1	1076	89	0.0	0.512
	2	245	55	7.3	0.025	2	1079	86	0.1	0.487
	4	277	55	38.8	3.7E-09	4	1097	82	15.0	2.8E-04
	3	334	66	106.9	6.1E-24	6	1154	75	64.5	5.2E-15
	5	358	69	134.6	5.9E-30	3	1160	87	82.7	5.6E-19
	6	395	58	160.4	1.4E-35	5	1193	80	109.0	1.1E-24
	7	409	62	176.9	3.8E-39	9	1195	84	114.7	6.4E-26
	9	430	64	200.5	2.8E-44	7	1233	70	139.1	3.3E-31
	10	546	63	316.3	2.0E-69	10	1247	76	159.4	1.3E-35
	11	570	56	332.6	5.7E-73	11	1277	66	178.4	9.6E-40
	8	875	61	643.1	2.2E-140	14	1869	54	758.9	8.4E-166
	12	1188	65	960.0	3.4E-209	15	1899	44	779.2	3.2E-170
	14	1229	44	979.7	1.7E-213	8	2212	71	1118.5	6.8E-244
	13	1269	50	1026.0	1.6E-223	12	2416	76	1327.5	2.8E-289
	15	1357	33	1096.5	7.6E-239	16	2481	23	1339.6	6.7E-292
	17	1948	20	1675.3	0.0E+00	13	2596	47	1479.2	0.0E+00
	16	2622	20	2349.2	0.0E+00	17	2907	26	1768.9	0.0E+00
Space use within 95% home-range										
	1	1876	148	0.0	0.980	1	1199	146	0.0	0.782
	2	1889	142	7.8	0.020	2	1207	141	2.5	0.218
	4	1931	135	41.7	8.5E-10	4	1245	135	35.1	1.9E-08
	3	1942	126	43.4	3.7E-10	6	1283	129	67.2	2.0E-15
	5	1952	121	48.7	2.6E-11	3	1279	135	68.7	9.4E-16
	6	1966	130	72.1	2.2E-16	9	1327	127	109.6	1.2E-24
	9	1989	118	82.0	1.5E-18	5	1327	131	112.7	2.6E-25
	7	2022	106	103.6	3.2E-23	10	1374	120	149.2	3.1E-33
	10	2030	110	115.2	9.6E-26	7	1462	114	231.6	4.1E-51
	11	2112	94	182.2	2.7E-40	11	1514	103	272.2	6.0E-60
	8	2152	120	247.9	1.5E-54	8	1985	124	763.4	1.3E-166
	12	2231	98	305.4	4.8E-67	12	2106	110	871.1	5.6E-190
	13	2335	83	393.5	3.5E-86	13	2358	92	1104.8	9.6E-241
	14	2501	59	536.4	3.3E-117	14	2514	74	1243.4	7.8E-271
	15	2596	45	616.6	1.3E-134	15	2587	59	1301.0	2.4E-283
	17	2828	22	826.4	3.5E-180	17	3133	30	1817.7	0.0E+00
	16	2989	25	989.5	1.4E-215	16	3283	30	1968.0	0.0E+00

Space use within 50% core area									
1	975	83	0.0	0.840	2	970	100	0.0	0.963
3	989	74	4.3	0.097	1	974	103	7.2	0.026
2	986	78	5.8	0.046	4	982	96	9.0	0.011
5	994	72	7.8	0.017	6	991	93	14.5	0.001
9	1006	68	15.7	3.3E-04	3	996	95	21.1	2.5E-05
10	1012	67	20.8	2.5E-05	5	1001	92	23.6	7.1E-06
4	1011	71	23.7	5.9E-06	9	1014	90	34.2	3.7E-08
6	1017	68	26.0	1.9E-06	10	1022	85	37.2	8.0E-09
8	1041	59	41.2	9.5E-10	7	1136	75	141.2	2.1E-31
12	1053	58	52.7	3.1E-12	11	1164	71	164.6	1.8E-36
7	1053	61	56.0	5.8E-13	8	1160	85	175.5	7.4E-39
11	1077	57	75.4	3.6E-17	12	1193	76	199.1	5.6E-44
13	1110	47	98.4	3.6E-22	14	1287	60	277.7	4.9E-61
14	1129	47	117.6	2.5E-26	15	1354	49	333.3	4.0E-73
15	1178	40	159.6	1.9E-35	13	1384	58	372.9	1.0E-81
17	1239	23	204.1	4.0E-45	17	1608	26	564.4	2.6E-123
16	1289	22	252.6	1.2E-55	16	1784	27	741.7	8.5E-162

Note: See Table 1 for abbreviations of factors and Table 2 for description of models. All factors were standardized prior to analysis. The top ranked model with ΔDIC = 0 best approximates the data. DEV=Deviance, pD=effective number of parameters, weights=DIC model weights.

For both species, high support for complex models and poor support for simple models (nos. 11-17, weights < 0.9) (Tables 2 and 3) indicated that selection depends on the combined and interactive effects of habitat type, prey density, and temperature across spatial scales. Hence, hypothesis 1 was supported as both prey density and temperature determined home-range placement of both species. Hypothesis 2 was partly supported, as for both species habitat selection within 95% home-ranges was not solely determined by prey density. Hypothesis 3 was partly supported, as for both species habitat selection within 50% core areas was not solely determined by temperature.

Habitat-type specific predictions

We present here only the predictions for the habitat types that were preferred by both species, namely large wood deposits, dense pioneer vegetation, and island edge (Table 1). For predictions of avoided habitat types, see Appendices A and B.

Large wood deposits (LWD). Both species clearly placed home-ranges in areas that contained LWD (Fig. 2a,b). Within 95% home-ranges, *B. b. spinosus* preferentially used LWD with high prey density whereas *B. viridis* used LWD independent of prey and temperature (Fig. 2c,d). Within 50% core areas, *B. b. spinosus* preferentially used LWD with high prey density, whereas *B. viridis* used LWD with lower temperatures (Fig. 2e,f). The selection probability decreased from large scales (home-range placement) towards small scales (50% core areas). Differences in selection between species were most pronounced at the smallest spatial scale. Confidence intervals increased from large towards small scales, indicating predictions to be most precise for home-range placement (Fig. 2).

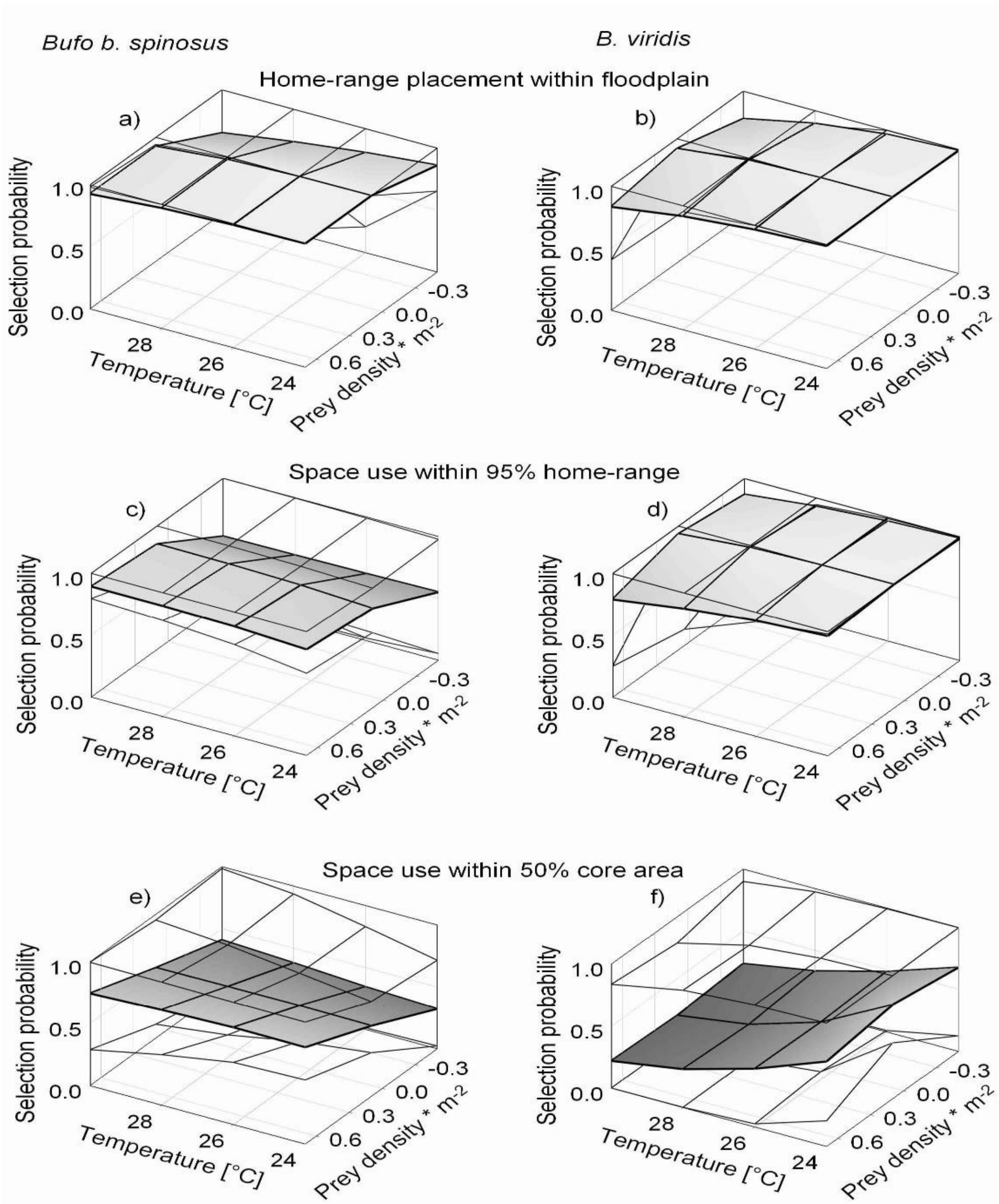

Figure 2. Predicted selection probabilities in relation to habitat type of large wood deposits, log-prey density, and temperature, separately by species and scale. The model that best explained habitat selection was used to predict selection probabilities (see Table 3). Predictions were done for constant low (-0.5), intermediate (0.1), and high log-prey density (0.7) as well as for 14 temperature values ranging from 20°C to 46°C. Shaded areas are mean selection probabilities, whereas transparent areas indicate the lower and upper 95% confidence interval. If there is no selection, the selection probability (P) is 0.5, if there is avoidance P < 0.5, and if there is preference P > 0.5. When the shaded area (selection surface) parallels the x- and y axes, selection is independent of prey and temperature.

Pioneer vegetation (PV). B. b. spinosus placed home-ranges in areas that contained PV with high prey density, whereas *B. viridis* placed home-ranges in areas that contained PV largely independent of prey density (Fig. 3a,b). These patterns were consistent within 95% home-ranges (Fig. 3c,d). Within 50% core areas *B. b. spinosus* preferably used PV with high prey density and high temperature (Fig. 3e). *B. viridis* instead used PV with low temperature rather than high prey density (Fig. 3f). Hence, differences in habitat selection between and within species were evident across spatial scales (Fig. 3).

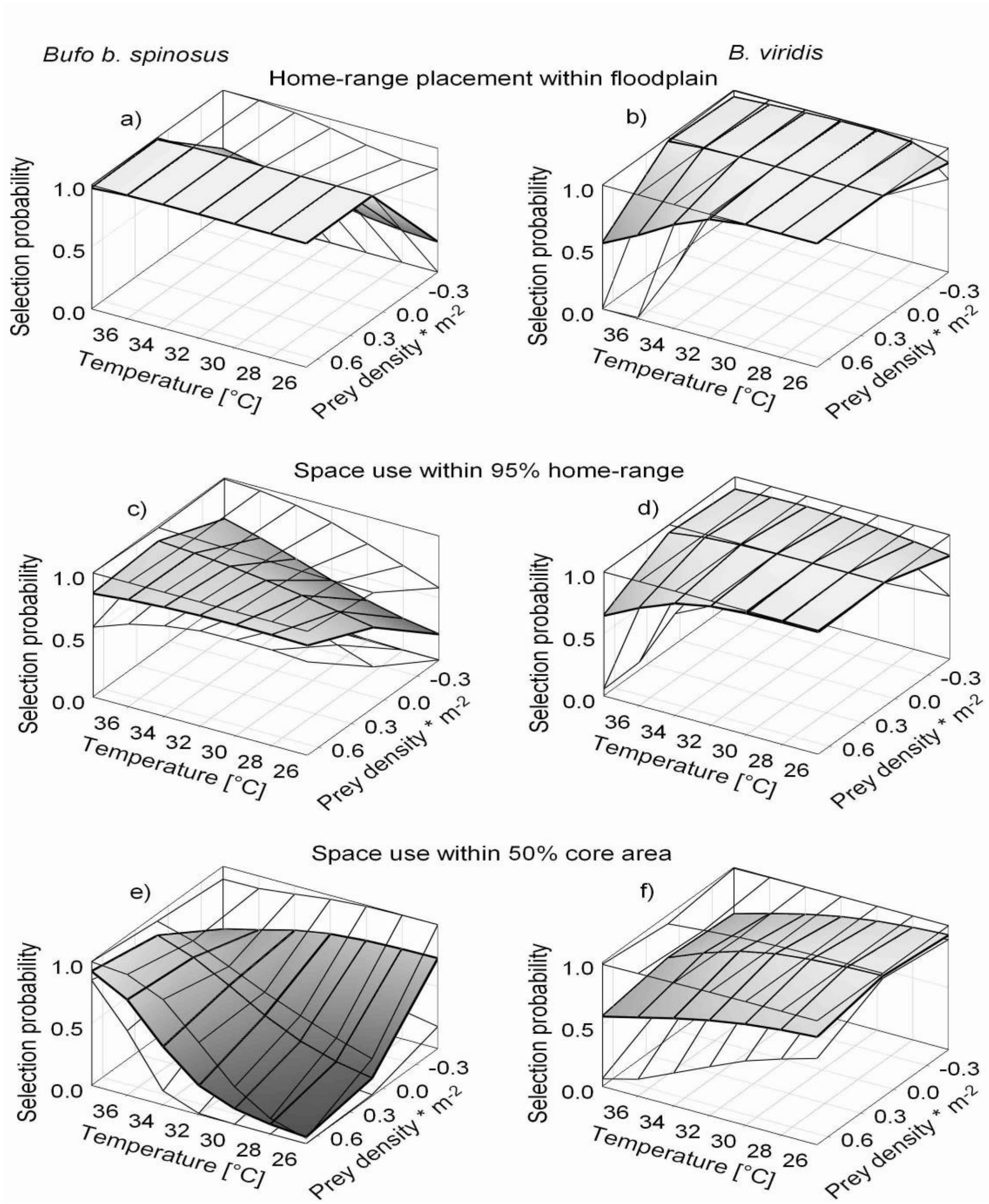

Figure 3. Predicted selection probabilities in relation to habitat type of dense pioneer vegetation, log-prey density, and temperature, separately by species and scale. The model that best explained habitat selection was used to predict selection probabilities (see Table 3). See legend of Fig. 2 for further details.

Island edge (ISLE). Both species used ISLE differently across spatial scales (Fig. 4). *B. b. spinosus* placed home-ranges in areas containing ISLE independently of prey and temperature (Fig. 4a). Similarly did *B. viridis*, except that it avoided ISLE with low prey density and low temperature (Fig. 4b).

Within 95% home-ranges, *B. b. spinosus* used ISLE with lower temperatures (Fig. 4c), whereas *B. viridis* used ISLE with high prey density (Fig. 4d). Within 50% core areas, *B. b. spinosus* used the coolest ISLE with lowest prey density (Fig. 4e). *B. viridis,* in turn, preferentially used the coolest ISLE with highest prey density (Fig. 4f).

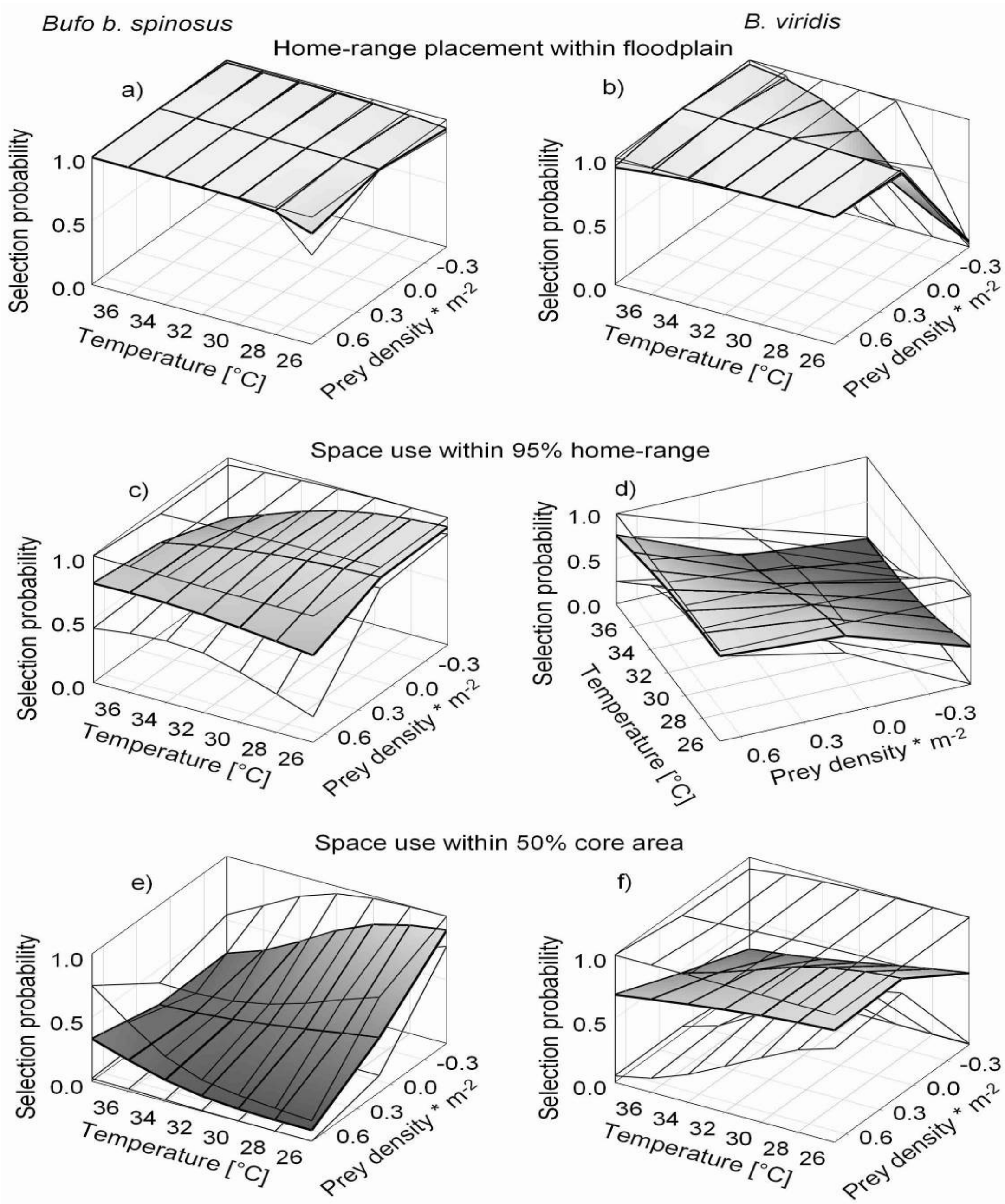

Figure 4. Predicted selection probabilities in relation to habitat type of island ege, log-prey density, and temperature, separately by species and scale. The model that best explained habitat selection was used to predict selection probabilities (see Table 3). See legend of Fig. 2 for further details.

In summary, both species used the same habitat types differently in relation to prey density and temperature across spatial scales, supporting hypothesis 4.

Discussion

Differential habitat selection is a central component in the ecology of species because it determines distribution and abundance, but it has proven difficult to measure empirically. We quantified the selection of terrestrial summer habitat of two sympatric amphibians (*Bufo b. spinosus* and *B. viridis*) as a function of habitat type, a biotic (prey density) and an abiotic resource (temperature) at three spatially hierarchical scales: i) home-range placement within a floodplain, ii) space use within 95% home-ranges, and iii) space use within 50% core areas (about 10% of the size of 95% home-ranges).

Placement and use of terrestrial home-ranges

We formulated four *a priori* hypotheses based on the assumption that food and temperature are most important in the terrestrial summer habitat of amphibians, and three concepts: first, because home-range placement determines the number of patches for exploitation and therefore resource availability (Johnson 1980), home-range placement is considered most important and controlled by all essential resources (Rettie and Messier 2000). Subsequent space use within home-ranges is conditional on home-range placement, and therefore controlled by less important or a subset of resources. Second, the selection of certain resources may be facilitated within home-ranges where the environment is better perceived than at larger spatial scales (Levins 1968, Orians and Wittenberger 1991). Third, as different resources are rarely equally distributed and overlapping, animal behaviors may segregate spatially (Marzluff et al. 2001). We therefore hypothesized that (1) both prey density and temperature determine home-range placement within the floodplain; (2) prey density determines space use within 95% home-ranges, which are assumed to mainly integrate spacious foraging behavior; (3) temperature determines space use within 50% core areas which are assumed to mainly integrate confined resting behavior (i.e. thermal conditions within a refuge are important); and (4) species select shared habitat types differently in relation to prey density and temperature across three spatially hierarchical scales, as it would allow the two species to coexist. The partial support for these hypotheses is discussed in turn.

We found that the factors hypothesized (prey density, temperature) to be important in the terrestrial summer habitat were indeed important. Both amphibian species placed home-ranges within the floodplain where prey density was slightly higher and temperature significantly lower than outside home-ranges (Table 1). Hence, resource gradients most likely control the distribution of the two species, in line with previous findings on birds and mammals (Collins 1985, Bennetts and Kitchens 2000, Eide et al. 2004). This finding fully constitutes hypothesis 1 and partly constitutes hypothesis 2 and 3 as the most complex model, including the combined and interactive effects of habitat type and resources, best explained habitat selection across spatial scales (Table 3). This result implies that amphibians perceive resource gradients at all spatial scales. Furthermore, all hierarchical scales may be of similar importance in the regulation of behaviors, e.g. resting and foraging, a finding that differs from previous studies on woodland caribou (Rettie and Messier 2000) and grizzly bear (Ciarniello et al. 2007), and suggests that the perception of resource gradients is species-dependent.

Differential use of shared habitat types between species

Both species preferred the same habitat types, except that *B. viridis* avoided established islands (Table 1). We thus explored space use within preferred habitat types in relation to varying prey density and temperature by applying different predictions. We found that the same habitat types were differently used in relation to resource density by both species at all spatial scales, supporting hypothesis 4 (Figs. 2-4, Appendices A,B). Our findings suggest niche differentiation through differential resource selection within shared habitat types across multiple spatial scales as a mechanism that stabilizes the co-existence of *B. b. spinosus* and *B. viridis* in terrestrial summer habitats. Similarly, scale-dependent niche differentiation has been found recently in mosquito larvae (Gilbert et al. 2008).

At the level of home-range placement within the floodplain, selection probabilities within habitat types were high (near 1) and varied little in response to prey and temperature gradients (Figs. 2a,b, 3a,b, 4a,b). Hence, home-ranges were largely placed in areas based on the availability of specific habitat types rather than resources. This was surprising, because from model selection we learned that the most complex model, including the interacting effects of habitat type and resources, best explained habitat selection across spatial scales (Table 3). Obviously, the placement of home-ranges is not solely affected by the availability of habitat types and resources. Intrinsic factors such as genetic differences between species or conspicuous landmarks may affect home-range placement as well (Hutto 1985), while resource gradients, and learning and experience may affect home-range use (Wecker 1964, Wiens 1972). Indeed, within 95% home-ranges and 50% core areas selection probabilities varied strongly across habitat types in relation to resources. It shows that differences in species' food and thermal requirements become apparent mostly at smaller spatial scales.

The differential use of shared habitat types likely reflects the regulation of different behaviors such as feeding and thermoregulation (Figs. 2-4). For example, *B. b. spinosus* may have selected island edges within 50% core areas for thermoregulation while *B. viridis* used island edges for feeding and thermoregulation (Fig. 4e,f). Similarly, *B. b. spinosus* likely used large wood deposits within 50% core areas for feeding while *B. viridis* selected large wood deposits most probably for thermoregulation (Fig. 2e,f). Large wood deposits were clearly preferred by both species and provided lowest temperature but also low prey density (Table 1). For *B. viridis*, large wood deposits are often the only habitat type in a matrix of exposed gravel sediment, and therefore are crucial in providing thermal refuge. However, large wood deposits occupied by *B. b. spinosus* were mostly in or close to established islands where prey density was high and temperature low (Table 1). Our results indicate that the interplay of habitat composition and resource gradients may affect habitat selection as well, thereby flagging an area of future research.

We partly observed highest selection probabilities when resource densities were non-optimal, i.e. prey density low and/or temperature was high (Figs. 3e, 4e). We need to quantify habitat-type specific growth rates and mortalities to better understand the high selection probabilities in ranges where resource density is non-optimal (Werner et al. 1983, Werner and Gilliam 1984).

The main result of our study is that the two amphibians (*B. b. spinosus* and *B. bufo*) differentiated their niche in terrestrial habitats by differential resource use within shared habitat types. As the same habitat type was used to regulate either foraging behavior or thermoregulation, the mechanistic basis of niche differentiation might be due to differences in physiological requirements. Similarly, Denton and Beebee (1994) hypothesized niche differentiation in *Bufo bufo* and *B. calamita* to be due to differences in physiology and foraging behavior rather than to competition. Our study goes one step further, as we showed that niche differentiation occurs at multiple spatial scales, namely within the floodplain, within 95% home-ranges, and within 50% core areas.

Conclusions

Our results demonstrate that the two sympatric amphibians selected habitats because of the combined and interactive impacts of habitat type, a biotic (prey density) and an abiotic resource (temperature) across spatial scales. It suggests that the two toad species perceive resource gradients at various spatial scales and distribute themselves along them. Furthermore, all spatial scales may be of similar importance for regulating foraging behavior and thermoregulation.

Both species largely preferred the same habitat types. However, the same preferred habitat types were differently used for foraging and thermoregulation across spatial scales, indicating differences in the physiological and behavioral requirements of the two toads. Niche differentiation through differential resource selection at multiple spatial scales might be an explanation why the two amphibians co-occur in the terrestrial summer habitat.

Differential resource selection between species was most evident at the smallest spatial scale considered (50% core area), highlighting its importance for feeding and thermoregulation. From a management perspective, it is particularly crucial to include core areas in habitat selection studies. Methodologically, our study contributes to the field by presenting a novel resource-selection function. This function integrates variation in habitat selection among individuals, thereby avoiding bias in results and facilitating the detection of habitat selection.

We quantified habitat selection of toads occurring in a pristine dynamic and complex floodplain. Our results can serve as a basis to better understand human-caused actions to floodplains in the selection of terrestrial habitat by amphibians. This understanding is in need, as floodplains were once widespread in Central Europe but today are among the most critically endangered ecosystems (Tockner et al. 2008) and amphibians are undergoing a global decline (Stuart et al. 2004).

Acknowledgements

We are grateful to Marianne Gehring and Wendelin Wehrle for field data collection, to Urs Richard for help with the raster data, and to Christopher Robinson for language polishing. All methods applied conform to the ethical and animal care guidelines issued by national (Ministerio dell'Ambiente e della Tutela del Territorio, Direzione per la Protezione della Natura, Roma) and the regional (Direzione Centrale Risorse Agricole, Forestali e Naturali, Regione Friuli Venezia Giulia, Udine) authorities in Italy that kindly provided permits. The project was funded by the MAVA Foundation (Switzerland).

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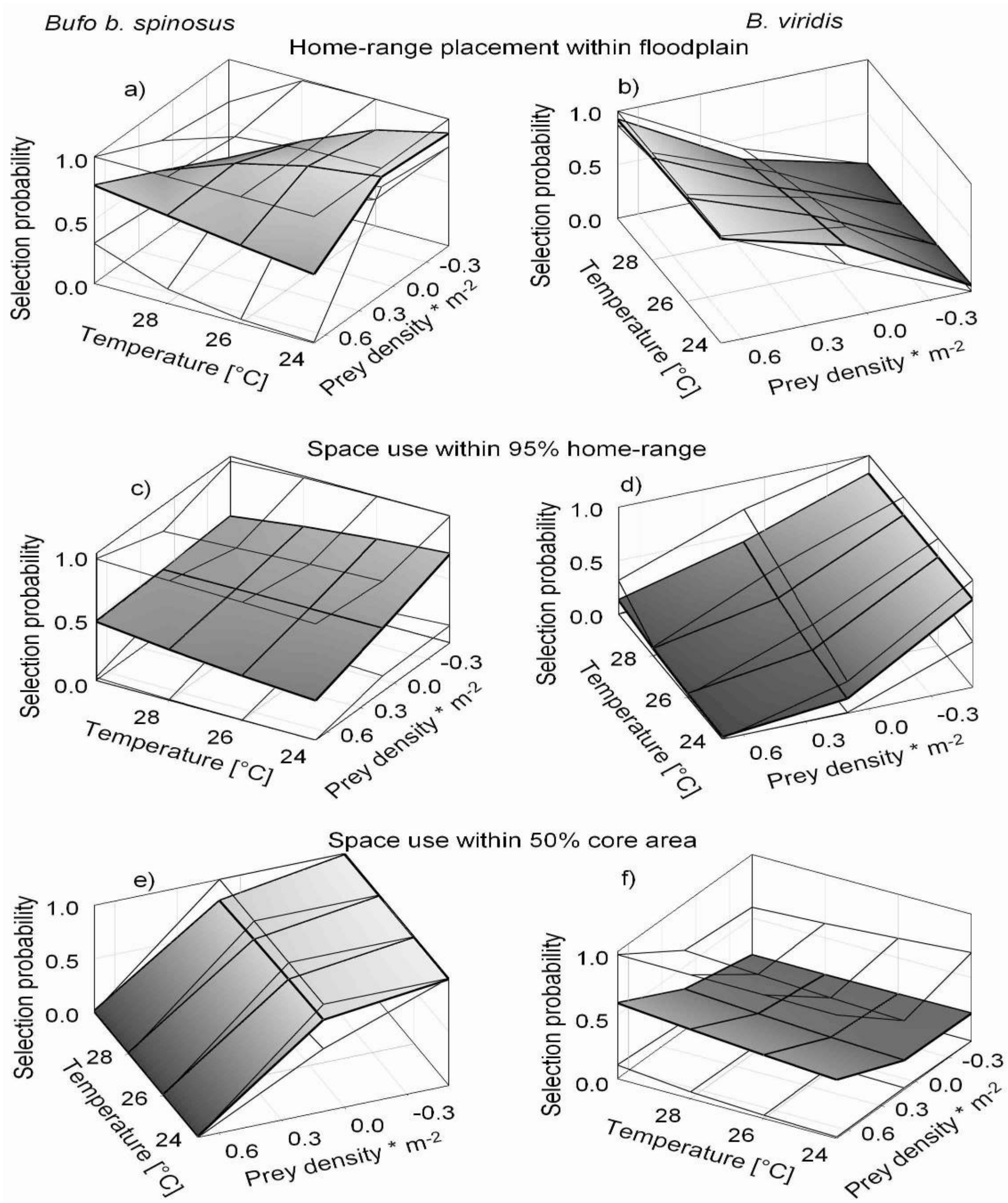
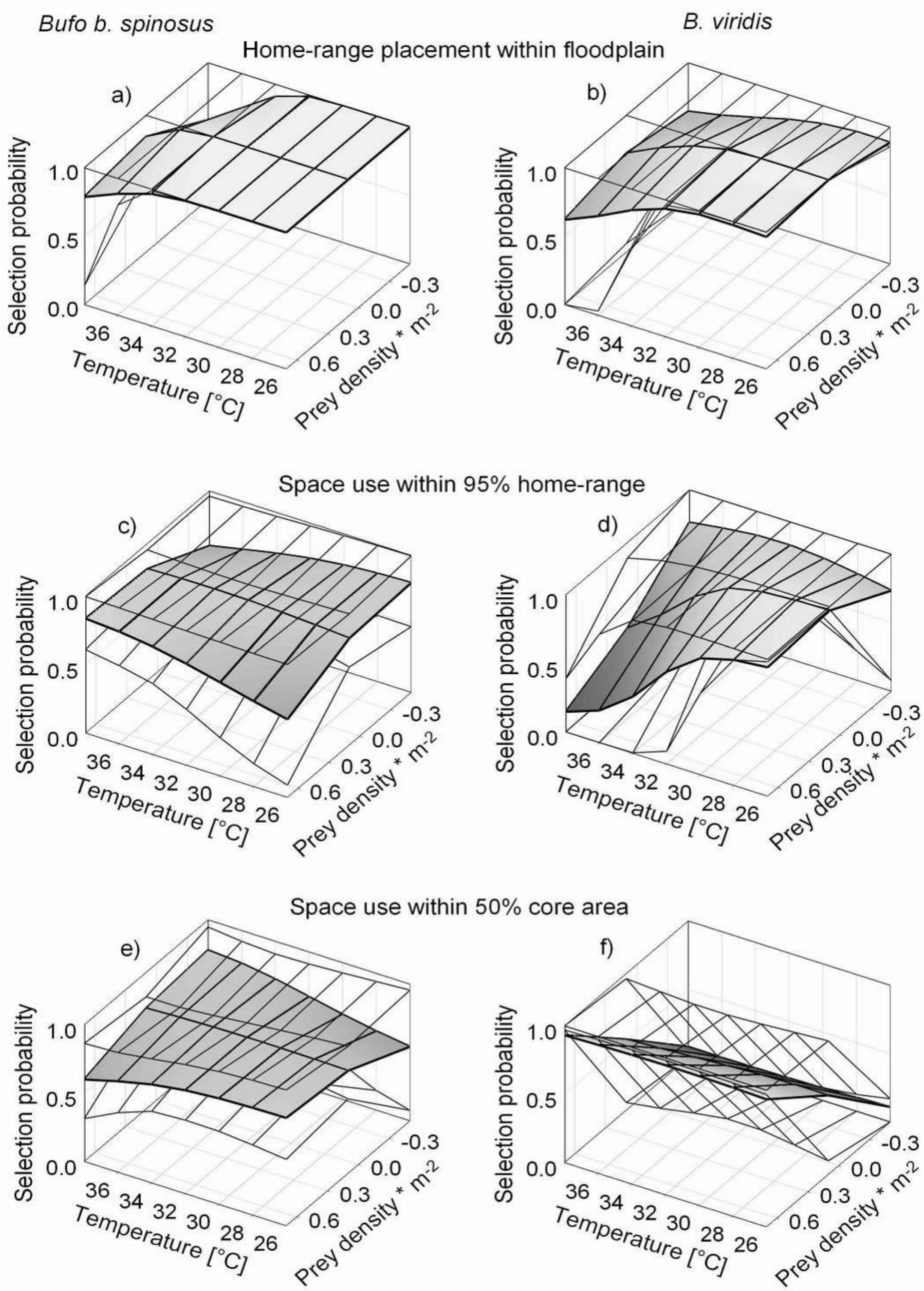
Appendix A. Predicted selection probabilities in relation to habitat type of exposed gravel sediments, log-prey density, and temperature, separately by species and scale. The model that best explained habitat selection was used to predict selection probabilities (see Table 3). See legend of Fig. 2 for further details.



Appendix B. Predicted selection probabilities in relation to habitat type of established islands, log-prey density, and temperature, separately by species and scale. The model that best explained habitat selection was used to predict selection probabilities (see Table 3). See legend of Fig. 2 for further details.



CHAPTER 4

Differential response to abiotic factors and predation risk rather than avoidance of competitors determine breeding site selection by four anurans in a pristine floodplain

Lukas Indermaur, Michael Schaub, Jukka Jokela, Klement Tockner, and Benedikt R. Schmidt

2008. Submitted

Abstract. Co-existence of species has been a central debate in ecology for decades but the mechanisms that allow co-existence are still a heatedly disputed topic. The main paradigms in ecology have shifted among the importance of inter- and intraspecific competition, predation and abiotic factors as determinants of community structure. Anuran communities allow examination of the importance of ecological vs. abiotic processes to explain local co-existence of species. In anurans, previous studies have shown that breeding site selection by reproductive females has important fitness consequences for developing tadpoles. Differential habitat selection is considered to reduce competition and hence allow co-existence, but the question calls for a detailed analysis. Here, we quantified breeding site selection of two pond-breeding toad (*Bufo bufo spinosus, B. viridis*) and two frog species (*Rana temporaria, R. latastei*) in relation to the separate and combined effects of landscape composition, hydrogeomorphology, abiotic and biotic conditions in ponds scattered patchily on a dynamic floodplain.

The rate of co-occurrence of *B. b. spinsous* with frogs was 17.3% and with *B. viridis* 12.4%, and all four species co-occurred in 1.5% of the sites. Co-occurrence rates were higher than expected based on neutral processes. Neutral means that all species are identical in their ecology. Landscape composition, hydrogeomorphology, abiotic and biotic factors jointly affected breeding site selection. While breeding site selection was species-specific and guided by abiotic and biotic factors, it was not affected by the presence of other anuran species. Abiotic conditions and pond size affected breeding site selection of toads, but not frogs. *B. b. spinosus* and *R. latastei* favored high predation risk ponds while *B. viridis* and *R. temporaria* avoided them. Hence, our results do not support the role of competition avoidance in governing current breeding site selection. We provide evidence that differential habitat use and differences in response to abiotic factors and predation risk together may override competitive interactions, thereby facilitating local co-existence of species. Our main result is that "life attracts life", which indicates that characteristics of the favourable ponds covary among anurans and fish. Ponds that allow high local diversity of freshwater communities are large, deep, warm, and structurally complex.

Introduction

Identifying the factors that promote co-existence of species has been a central debate in all key ecological paradigms for decades (Gause 1934; Gliwicz and Wrzosek 2008; Hairston 1951; Hairston 1980; Hutchinson 1959; Pianka 1967). The main controversy has been on the importance of biotic vs. abiotic processes in controlling the local and regional co-existence of species. For example, do competitive interactions exclude species from their potential ranges (Gause 1934; Hardin 1960), or are species ranges more affected by predation risk (Gallet et al. 2007; Jiang and Morin 2005; Menge and Sutherland 1976)? Abiotic constraints surely limit the distribution patterns of species (Chesson 2000; Connell 1979; Dunson and Travis 1991; Matias et al. 2007), but how important are abiotic factors at the local scale? In attempts to explain distribution patterns across large regions some success has even been made by assuming that all species are ecologically equivalent (e.g. “neutral”) (Hubbell 2001; Muneepeerakul et al. 2008; Tilman 2004).

We postulate that most ecological and abiotic processes that determine co-existence of species occur at local scales, i.e. within- and among those habitat patches that are within the range of individual habitat choice. It is in this local scale, rather than regional, where alternative processes proposed to explain species co-existence are best studied (Enright et al. 2007). In this study, our goal is to explore whether local breeding site selection of anuran species leads to co-existence, and whether it is determined by differential preferences for the abiotic and/or biotic environment.

The maternal selection of breeding site is a crucial step in the complex life cycle of pond-breeding amphibians as it sets the scene for larval development, which in turn affects survival and fitness in the terrestrial stage (Altwegg and Reyer 2003; Berven 1990; Rieger et al. 2004; Schmidt et al. 2008; Semlitsch et al. 1988). The emerging view of studies focusing on breeding site selection is that abiotic and biotic factors (mainly predation risk) jointly affect breeding site selection (Binckley and Resetarits 2008; Denoël and Lehmann 2006; Knapp et al. 2003; Laurila 2000; Pellet et al. 2004; Resetarits 2005; Richter-Boix et al. 2007; Van Buskirk 2003; Van Buskirk 2005). Among biotic factors, the role of interspecific competition in breeding site selection, however, may still be underappreciated (but see Resetarits and Wilbur 1989; Van Buskirk 2005). This is surprising, as competition is usually strong in larval communities; and there is consensus about the negative impacts of strong competition on larval performance (Morin and Johnson 1988; Semlitsch 1987a; Wilbur 1977). Hence, to understand the mechanisms underlying the co-existence of species, the direct effects of competitors, predators, and the abiotic environment on breeding site selection must be clarified.

Breeding habitat selection of species usually changes along several environmental gradients (Connell 1961; Wellborn et al. 1996). Changes in habitat selection highlight differences among species in tolerance to environmental factors. Hydroperiod is a major environmental gradient, which affects habitat selection and thereby co-existence of fresh water species (Wellborn et al. 1996). Short hydroperiods favour species with short development times and inferior competitive abilities. Long hydroperiods select for opposite characteristics (Wellborn et al. 1996; Wilbur and Collins 1973). Other factors covary with hydroperiod such as predation risk, temperature, and food availability (Wellborn et al. 1996; Wilbur 1987).

We studied breeding habitat selection in a dynamic, pristine floodplain, where ponds are distributed along gradients in hydroperiod, predation risk, and temperature (Indermaur et al. 2008a). Additionally, the floodplain has two main habitats. An active tract that is frequently reworked by floods, and the riparian forest that fringes the active tract. Ponds of the active tract are in general less variable in hydroperiod, warmer, and contain less predators than ponds in the riparian forest (Indermaur et al. 2008a). Hence, as all species could easily access all ponds along the environmental gradients we were able to explore whether differential habitat preferences facilitated co-existence of species. Our study differs from previous studies in several ways. First, we study a patchily distributed community of pond breeding anuran species, where local breeding communities are not limited by dispersal. This is an important precondition to separate the effects of competitive interactions and geographic distances between ponds on species' occurrence (Hanski and Gilpin 1997). Second, we evaluated whether pond selection depended on the presence of other species in addition to other biotic and abiotic factors. A subset of factors that we focused on here, were shown to affect larval performance (growth, body size) in a previous study (Indermaur et al. 2008a). We were therefore able to separate competitive effects from other biotic and abiotic factors as well as to link pond selection to larval performance. Third, we studied habitat selection of amphibians in a pristine environment, where the life history and ecology of many amphibians most likely evolved. Otherwise, historical processes such as the transformation of landscapes by humans may mask the processes that determine habitat selection of species (Piha et al. 2007). Finally, our analysis of breeding site selection takes into account that species are detected imperfectly (Gu and Swihart 2003; Schmidt 2004).

We quantified the separate and combined impacts of the abiotic and biotic factors on breeding site selection of four anuran species occurring in a dynamic floodplain. Abiotic factors included landscape context, hydrogeomorphology, and abiotic conditions. The biotic environment included the abundance of predators, and the presence of competitors. Our main goals were i) to explore whether species selected different habitat types; and ii) to explore whether species select the same habitat types differently in relation the abiotic and biotic environment; and iii) to evaluate whether competitive effects determine pond selection rather than the abiotic environment and predation risk. Answers to these questions shed light on the mechanisms that facilitate the co-existence of species. Our results serve as a reference point to amphibian population management in human altered landscapes, and this is where most European amphibian species occur nowadays (Waringer-Löschenkohl et al. 2001).

Methods

Study site

The study was conducted from February 1 until July 30, in 2005 and in 2006, in an island-braided floodplain along the 7th order Tagliamento River in northeastern Italy (46°N, 12°30'E). The Tagliamento (catchment area: 2580 km^2) originates at 1000 m asl in the southern fringe of the European Alps and flows almost unimpeded by dams for 172 km to the Adriatic Sea. Unlike most European rivers, the river retains its essentially pristine morphological and hydrological characteristics (Ward et al. 1999).

The study site (river-km 79.8 -80.8; 135 m asl) covered a 800 m wide active tract and the adjacent riparian forest (right bank). The active tract comprised a spatiotemporally complex mosaic of vegetated islands, a braided network of main and secondary channels, backwaters and ponds, embedded within a matrix of exposed gravel sediments (Indermaur et al. 2008a; Petts et al. 2000)(chapter 1, Fig. 1; chapter 5 Fig. 1). Within the riparian forest (right bank), ponds are distributed along an abandoned alluvial channel. The steep hillslope of Monte Ragogna borders the left bank of the floodplain.

The habitat mosaic within the study area is frequently reworked by floods with highest peaks in autumn and additional peaks during snow melt in spring (Tockner et al. 2003). This river section was chosen because both habitat heterogeneity (Arscott et al. 2002) and amphibian diversity are highest (Tockner et al. 2006).

Study species

Out of eleven species that were present in the study section we selected the four most abundant species to estimate probabilities of occurrence and the factors that affect these probabilities: The European common toad (*Bufo bufo spinosus*), the Green toad (*B. viridis*), the European common frog (*R. temporaria*), and the Italian Agile frog (*R. latastei*).

Bufo b. spinosus is a ubiquitous species typically spawning in permanent natural and man-made ponds (Giacoma and Castellano 2006). *Rana temporaria* is a widespread species that occurs across a wide altitudinal range. In Italy, *R. temporaria* is often found in cool wooded areas adjacent to running waters (Giacoma and Castellano 2006). *R. latastei* is a characteristic lowland species that prefers vegetated ponds containing subsurface structures for egg attachment (Giacoma and Castellano 2006). However, *R. latastei* also spawns in temporary ponds in open areas. *Bufo viridis* is a pioneer species preferring warm and shallow ponds of early succession stages (Giacoma and Castellano 2006).

The frogs (*R. temporaria*, *R. latastei*) start breeding in February, followed by *B. b. spinosus* in March, and by *B. viridis* in late April. The breeding period of frogs is constrained to a few weeks. *Bufo b. spinosus* extends the breeding period from weeks to months depending on the predictability of the environment (Kuhn 1993). Similarly, *B. viridis* colonizes ponds that fill at high water levels until late July (L. Indermaur, *personal observation*).

Field methods

Pond selection. 353 ponds (pooled data of 2005: n = 170 and 2006: n = 183) with pond surface area ≥ 1 m^2 and water depth > 0.05 m were selected for the study. Backwaters were also included, and their surface water area was defined as the conjunction to side channels. Ponds were located in the riparian forest (n = 123; pooled data), at the forest edge (n = 55), which is the interface between the forest and the active tract, at the edge of vegetated islands within the active tract (n = 97), as well as in exposed gravel sediments of the active tract (n = 78).

We recorded egg clutches and larvae of *B. b. spinosus*, *B. viridis*, *R. temporaria*, and *R. latastei*. Each individual pond was surveyed at 10-day intervals between February 1 and July 30; 16 times in total. At each sampling date, two observers searched for egg clutches and larvae. The searching time was in proportion to pond surface area and structural complexity of the ponds. Larger ponds were waded through to improve detection. Visibility of egg clutches and tadpoles was in general high because of low turbidity.

Pond attributes. We used a set of abiotic and biotic factors to estimate probabilities of occurrence (Table 1). These factors included landscape composition (habitat type and shading), hydrogeomorphology (mean pond surface area and water depth, which were considered as surrogates for hydroperiod length; availability of structural elements for egg attachment), abiotic (pH; temperature), and biotic conditions (fish presence; predation risk; presence of other anuran species than of the focal species; egg density of other anuran species than of the focal species). The importance of these factors was supported by the published studies (Table 1). Details on sampling intervals and measuring methods are presented in Table 1. The factors "shading", "hydroperiod length", "algae cover", "specific conductance", "oxygen concentration" were finally omitted in the analyses to minimize collinearity of explanatory factors (Appendices A and B).

Table 1. Factors used for predicting the probability of occurrence and detection.

Process	Factor	Explanation	Sampling interval	Measuring detail	Reference
Probability of occurrence					
	YY	Year (2005,2006)			
Landscape composition					
	Ht	Habitat type/spatial location (4 levels: riparian forest, edge of riparian forest, exposed gravel, island edge)			Guerry and Hunter 2002; Kolozsvary and Swihart 1999
	(Sh)	Shading [%]	Monthly (4 times)	Visually	Pellet et al. 2004
Hydrogeomorphology					
	Ar[a]	Pond surface area [m^2]	Monthly (4 times)	dGPS (Trimble GeoXT, Zurich)	Beja and Alcazar 2003; Laurila 2000
	De[a]	Water depth [m]	Weekly	Maximum water depth	Beja and Alcazar 2003; Pearman 1993
	St	Availability of structural elements for egg attachment: branches, aquatic vegetation [%]	Monthly (4 times)	Visually	Jansen and Healey 2003; Mazerolle et al. 2005; Vos and Stumpel 1995
	(Hp)	Hydroperiod length [d], i.e. # days ponds contained water	Weekly		Denver et al. 1998; Semlitsch 1987b; Wilbur and Collins 1973
Abiotic condition					
	pH[a]	pH [H^+]	Monthly (4 times)	WTW pH 340[b]	Beebee 1986; Cummins 1986
	T[a]	Mean maximum temperature °C	Hourly	Thermochron ibutton Htggers DS1921G	Herreid and Kinney 1967; Negovetic et al. 2001
	(Al)	Algae cover [%]	Monthly (4 times)	Visual quantification of algae cover	Mallory and Richardson 2005; Peterson and Boulton 1999
	(Cy)	Specific conductance [µS/cm]	Monthly (4 times)	WTW LF 340[b]	Knutson et al. 2004 ; Pellet et al. 2004
	(Ox)	Oxygen concentration [mg/l]	Monthly (4 times)	WTW Oxi 340[b]	Wassersug and Seibert 1975
Biotic condition					
	Fi	Fishes ≥ 10 cm (present/absent)	Monthly (4 times)	Visually	Joly et al. 2001; Knapp et al. 2003
	Pr[c]	Predation risk (index: 0-1)[b]	Once	Sweep netting and funnel traps proportional to pond surface area	Knutson et al. 2004; Skelly and Werner 1990
	Pbb	Presence of *Bufo b. spinosus* (0,1)	Weekly	Visually	
	Pbv	Presence of *B. viridis* (0,1)	Weekly	Visually	
	Pte	Presence of *Rana temporaria* (0,1)	Weekly	Visually	
	Pla	Presence of *R. latastei* (0,1)	Weekly	Visually	
	(Ebb)	*n* egg clutch of *Bufo b. spinosus*/m^2	Weekly	Visually	
	(Ebv)	*n* egg clutch density of *B. viridis*/ m^2	Weekly	Visually	
	(Ete)	*n* egg clutch density of *Rana*	Weekly	Visually	

		temporaria/ m^2		
	(Ela)	*n* egg clutch density of *R. latastei*/ m^2	Weekly	Visually
Probability of detection				
	YY	Year (2005,2006)		
	Day[a]	Day in the season		
	Ar[a]	Pond surface area [m^2]	s. above	
	De[a]	Water depth [m]	s. above	
	Si	Site (two levels: riparian forest, active tract)		

Note: Factors in brackets were not used for modelling as they were highly correlated with other factors (see Appendices A and B).

[a] Factor that were also modelled as quadratic terms to reflect non-linear responses of species to environmental factors.

[b] Wissenschaftlich-Technische Werkstätte GmbH, Weilheim, Germancy.

[c] Sum of individuals of newts (*Triturus carnifex, T. vulgaris*), snakes (*Natrix natrix*), insects (larvae and adults of *Dytiscus marginalis, Aeshna sp.*)*number of predator groups present (newts, snakes, insects), normalized between 0 and 1. The weighting factor "number of predator groups" was included as the interactive effects of various predator taxa are considered more dangerous than of single taxa.

Statistical analyses

Model selection. We used a model selection approach to identify appropriate statistical models for estimating probabilities of detection (p) and occurrence (ψ) (Burnham and Anderson 2002; MacKenzie et al. 2002). The data were analysed in two steps. First, we estimated p per species. Second, we used the model that best explained p to find a model that best explains ψ.

p-models. Species detection was not always guaranteed. Therefore, we used statistical methods that account for imperfect detection (MacKenzie et al. 2002). The factors used to estimate p included seasonal (year, day in the season), and spatial components (pond surface area, site) (Table 1, Appendix C). Factors day and pond surface area were also included as quadratic effects.

Ψ-models. The analysis of pond occupancy (ψ) was done in three steps. First, we assigned explanatory variables to four groups: landscape composition, hydrogeomorphology, abiotic and biotic conditions (Table 1). We first formulated models per factor group (Appendix D). Models included both linear and quadratic effects. In the second step, we formulated models that combined linear factors of multiple factors groups. In the third step, we formulated models that combined linear and quadratic factors of multiple factor groups. These models hypothesized that ψ changes nonlinearly. Factor year was used in every model to correct for its potential effects.

Model fitting. For estimation of p and ψ we used R (R development core team 2005) package RMark (V1.8.0) (Laake und Rexstad 2008) to construct linear models for program MARK (White and Burnham 1999). All continuous explanatory factors were z-standardized prior to analysis and factor habitat type (4 levels) was taken as the intercept.

Goodness of fit. Using software PRESENCE v2 (Hines 2006), we performed a goodness of fit test (MacKenzie and Bailey 2004) to evaluate whether our p and ψ -models fit the data. Goodness of fit testing was done separately for each species. The assumption is that every simpler model in the set will fit the data if the most complex model does, if its Akaike Information Criterion is smaller than of the most complex model. A model is considered to fit the data if the variance inflation factor ($\hat{c} = \chi^2 / df$) is less than 3. The fit for the best selected models varied among species (*B. b. spinsous*: $\hat{c}$ = 5.51; *B. viridis*: $\hat{c}$ = 1.41; *R. temporaria*: $\hat{c}$ = 1.68; *R. latastei*: $\hat{c}$ = 9.34). We used the estimated variance inflation factor to adjust model selection criteria and standard errors of the parameters (Burnham and Anderson 2002).

Predictions. Because there was considerable model selection uncertainty (see Results), we used model averaging techniques (Burnham and Anderson 2002). Using model averaged slopes and standard errors we predicted the relationship between explanatory factors and ψ. The intercept was the slope of the habitat type “forest edge”. This habitat type was used similarly by all species.

Results

Pond characteristics. We observed distinct environmental gradients in all pond characteristics from the riparian forest towards the forest edge, and from the forest edge towards the active tract that contained the habitat types exposed gravel and island edges. For example, pond surface area, pH, and temperature increased, while hydroperiod length, predation risk, and availability of structural elements for egg attachment decreased from the riparian forest towards the active tract (Table 2). Ponds were deeper in the riparian forest and at island edges than in the active tract. Large and shallow ponds were characteristic for exposed gravel sediments in the active tract (Table 2). They exhibited high temperature and pH, and low predation risk, as well as limited structural elements for egg attachment. In the riparian forest and at the forest edge, the length of the hydroperiod was on average one week shorter than of ponds in the active tract (but see Indermaur et al. 2008a).

Table 2. Descriptive statistics for various factors, separately for different spatial locations in the floodplain.

Location in the floodplain/factor		Mean	SD	Range	
Forest (n = 123)					
Ar	Pond surface area	56.143	81.065	0.156	435.691
De	Water depth	0.344	0.291	0.010	1.545
Ebb	Egg density *Bufo bufo*	0.094	0.162	0.000	1.061
Ebv	Egg density *B. viridis*	0.002	0.019	0.000	0.204
Ela	Egg density *Rana latastei*	1.127	3.267	0.000	32.889
Ete	Egg density *R. temporaria*	0.196	0.677	0.000	6.024
Hp	Hydroperiod length	99.600	17.480	5.000	106.000
Ph	pH	7.800	0.311	6.940	8.528
Pr	Predation risk	0.249	0.277	0.000	1.000
St	Structural elements	74.942	20.691	0.000	100.000
T	Temperature	18.974	3.762	12.050	31.600
Forest edge (n = 55)					
Ar	Pond surface area	70.752	124.089	0.251	515.619
De	Water depth	0.263	0.260	0.001	1.333
Ebb	Egg density *Bufo bufo*	0.063	0.230	0.000	1.624
Ebv	Egg density *B. viridis*	0.004	0.017	0.000	0.093
Ela	Egg density *Rana latastei*	0.443	1.042	0.000	4.775

Ete	Egg density *R. temporaria*	0.160	0.737	0.000	5.143
Hp	Hydroperiod length	94.58	19.81	35.000	106.000
Ph	pH	7.813	0.287	6.885	8.605
Pr	Predation risk	0.101	0.188	0.000	0.683
St	Structural elements	63.370	20.142	0.000	100.000
T	Temperature	19.129	4.098	12.200	27.354
Island edge (*n* = 97)					
Ar	Pond surface area	72.961	205.278	0.087	1542.129
De	Water depth	0.305	0.277	0.000	1.091
Ebb	Egg density *Bufo bufo*	0.150	0.371	0.000	1.899
Ebv	Egg density *B. viridis*	0.011	0.044	0.000	0.320
Ela	Egg density *Rana latastei*	0.166	0.595	0.000	5.314
Ete	Egg density *R. temporaria*	0.090	0.268	0.000	1.699
Hp	Hydroperiod length	87.900	24.70	8.000	106.000
Ph	pH	7.926	0.234	7.340	8.575
Pr	Predation risk	0.018	0.043	0.000	0.226
St	Structural elements	65.609	18.998	0.000	100.000
T	Temperature	21.476	4.461	13.000	30.100
Exposed gravel (*n* = 78)					
Ar	Pond surface area	169.258	373.616	0.236	2213.652
De	Water depth	0.220	0.182	0.004	1.041
Ebb	Egg density *Bufo bufo*	0.049	0.156	0.000	1.162
Ebv	Egg density *B. viridis*	0.025	0.082	0.000	0.627
Ela	Egg density *Rana latastei*	0.085	0.389	0.000	3.162
Ete	Egg density *R. temporaria*	0.028	0.200	0.000	1.760
Hp	Hydroperiod length	87.22	26.86	3.000	106.000
Ph	pH	8.036	0.241	7.498	8.860
Pr	Predation risk	0.017	0.046	0.000	0.234
St	Structural elements	46.874	26.058	0.000	100.000
T	Temperature	21.643	4.659	13.200	32.400

Note: see Table 1 for description of factors.

Occurrence rates. Naïve occurrence rates (% of 353 ponds occupied) that are not corrected for imperfect detection were highest for *B. b. spinosus* (46.7%), followed by *R. latastei* (45.8%), *R. temporaria* (27.7%), and *B. viridis* (13.5%). All four species co-occurred in 1.5% of the ponds. *B. b. spinosus* exclusively co-occurred with the two frog species (*R. temporaria, R. latastei*) in 17.3% of the ponds. The two frog species exclusively co-occurred in 22% of the ponds, and the two toad species (*B. b. spinosus, B. viridis*) exclusively co-occurred in 12.4% of the ponds. Egg clutch densities of *B. b. spinosus* were highest in ponds at island edges, for *B. viridis* in exposed gravel sediments, and for *Rana temporaria* and *R. latastei* in the riparian forest (Table 2).

Model selection

Modelling detection (p). Models including seasonal effects (Year+Day+Day^2) explained the detectability of *B. b. spinsous* and *R. latastei* best (Akaike weights: 0.43 and 0.39, respectively) (Appendix C). Similarly, for *B. viridis* seasonal effects explained detection best (Day+Day^2) (Akaike weight: 0.45). The detection of *R. temporaria* depended on both spatial (pond surface area, site), and temporal components (Year+Day+Day^2) (Akaike weight: 0.48).

Per-visit probabilities of detection of frogs (*R. temporaria, R. latastei*) were highest (~99%-90%) from February until the end of March when frogs aggregated at breeding sites (Appendix E). Similarly, *B. b. spinosus* was detected best from February until the end of March (82%-67%). In early July, the detection probability was low as 7% for frogs and 40.4% for *B. b. spinosus*. The detection probability of *B. viridis*, a typical late breeder, increased from April to early July from 17% to 79%.

Modelling occurrence (ψ). For all species, there was uncertainty in model selection because several models explained ψ equally well (Table 3, Appendix D). For *B. b. spinosus*, model selection uncertainty was most pronounced. All factors were important. For *B. viridis*, all factors except predation risk and the presence of other species were important. For *R. temporaria*, all factors except temperature and pH were important. For *R. latastei* pond surface area, water depth, the availability of structural elements for egg attachment and the presence of fish were important.

Table 3. Model selection results for predicting the probability of occurrence, sorted after differences between Akaike's small sample information criterion (ΔQAICc), corrected for overdispersion with the variance inflation factor ($\hat{c}$). Only models with Akaike weights > 0.05, the constant model (#1) as well as the most complex model (#55) are shown for brevity. For the full model set, see Appendix D.

Mod. no.	Factors															*K*	ΔQAICc	Qweight	Qdeviance
Bufo b. spinosus: p = (YY+Day+Day^2), $\hat{c}$ = 5.51																			
32							T	T^2	Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	15	0.00	0.150	536.79
26		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2						15	1.02	0.090	537.80
9							T		Ph	Ph^2		Pr	Pbv	Pte	Pla	14	1.36	0.076	540.31
31							T	T^2	Ph	Ph^2	Fi					11	1.48	0.072	546.86
5		Ar		De		St	T		Ph	Ph^2						12	1.55	0.069	544.81
41	Ht						T	T^2	Ph	Ph^2	Fi					14	1.63	0.066	540.59
46		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi					16	2.06	0.053	536.67
1																6	7.48	0.004	561.02
55	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	23	11.98	0.000	530.94
B. viridis: p = (Day+Day^2), $\hat{c}$ = 1.41																			
16		Ar		De		St	T		Ph	Ph^2	Fi					12	0.00	0.279	539.78
43		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi					13	0.01	0.278	537.64
46		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi					15	1.78	0.115	535.09
44		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi					14	2.16	0.095	537.64
50	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi					16	3.04	0.061	534.17
55	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	22	11.95	0.001	529.71
1	(.)															5	84.56	0.000	639.00
Rana temporaria: p = (YY+Day+Day^2+Ar+Si), $\hat{c}$ = 1.68																			
58											Fi	Pr	Pbb	Pbv	Pla	13	0.00	0.487	1164.57
7		Ar		De		St					Fi	Pr	Pbb	Pbv	Pla	16	2.77	0.122	1160.84
4	Ht										Fi	Pr	Pbb	Pbv	Pla	16	3.06	0.106	1161.12
30		Ar	Ar^2	De	De^2	St					Fi	Pr	Pbb	Pbv	Pla	18	3.72	0.076	1157.38
55	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	25	11.90	0.001	1149.73
1																8	46.46	0.000	1221.63
R. latastei: p = (YY+Day+Day^2), $\hat{c}$ = 9.34																			
23		Ar		De		St										9	0.00	0.333	331.59
6		Ar		De		St					Fi					10	1.71	0.141	331.20
34		Ar	Ar^2	De	De^2	St										11	2.08	0.118	329.45
27		Ar	Ar^2	De		St					Fi					11	3.42	0.060	330.78
59	Ht	Ar		De		St										12	3.43	0.060	328.66
1																6	11.74	0.001	349.58
55	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	23	21.14	0.000	322.08

Note: See Table 1 for abbreviations of factors. (.) = constant probability of occurrence (ψ). The top ranked model with ΔQAICc = 0 best approximates the data and models with ΔQAICc ≤ 2 are considered to receive substantial support from the data. Number of factors (*K*) and Akaike weights are given. When one model receives weights ≥ 0.9 there is no model selection uncertainty apparent. Factor year was included in every model to correct for its potential impact.

Probabilities of occurrence (ψ). Probabilities of occurrence that are corrected for imperfect detection were close to the naïve rates of occurrence (see above). *Bufo bufo spinosus* occurred in 46.8% (SE 2.6%) of all ponds. *B. viridis* occurred only in ponds in the active tract (13.8% of all ponds, SE 1.85%). *Rana temporaria* occurred in 28.1% (SE 2.3%) and *R. latastei* occurred in 45.8% (SE 2.6%) of the ponds.

Occurrence of *B. b. spinosus* and *R. latastei* were equally likely across habitat types (Fig. 1A). Both, *B. viridis* and *R. temporaria* avoided ponds in the riparian forest. Both toad species preferred large ponds (Fig. 1B), while pond surface area was less important for frogs (i.e. confidence intervals included zero; Table 4). *B. viridis* preferred shallow ponds without structural elements for egg attachment (i.e. twigs, branches) while *R. latastei* preferred ponds with opposite characteristics (Fig. 1C,D). Abiotic conditions (temperature, pH) did not affect the occurrence of frogs (Table 4). Only the effects of temperature on ψ are graphically shown, as the factor pH included zero in confidence intervals for all species (Table 4). Both toad species preferred warm ponds while frogs tended to use cool ponds (Fig. 1E).

Table 4. Model averaged regression slopes (on the logit scale) that were used to predict probabilities of detection and occurrence.

	Bufo b. spinosus		*B. viridis*		*Rana temporaria*		*R. latastei*	
Factors	Beta	SE	Beta	SE	Beta	SE	Beta	SE
Probability of occurrence								
Year	-0.426	0.276	0.148	0.488	**0.944**	**0.305**	-0.077	0.290
Landscape context (intercept)								
Lo (forest)	0.187	0.260	**-4.694**	**0.770**	**-3.171**	**0.409**	0.019	0.248
Lo (forest edge)	**-0.233**	**0.072**	0.081	0.178	-0.121	0.106	-0.035	0.072
Lo (island edge)	-0.114	0.061	0.222	0.148	-0.020	0.093	**-0.278**	**0.068**
Lo (exposed gravel)	**-0.276**	**0.072**	0.248	0.151	**-0.298**	**0.129**	**-0.290**	**0.078**
Hydrogeomorphology								
Ar	**0.261**	**0.115**	**1.638**	**0.411**	0.173	0.118	0.046	0.239
Ar^2	**-0.038**	**0.017**	**-0.104**	**0.037**	-0.006	0.010	-0.042	0.024
De	**0.168**	**0.081**	**-1.195**	**0.491**	-0.082	0.081	**1.524**	**0.251**

De^2	**-0.053**	**0.019**	-0.007	0.083	**-0.033**	**0.016**	**-0.098**	**0.020**
St	**0.338**	**0.067**	**-1.261**	**0.341**	-0.027	0.072	**0.995**	**0.166**
Abiotic condition								
T	**1.119**	**0.170**	**1.378**	**0.321**	0.003	0.013	0.002	0.009
T^2	**-0.374**	**0.078**	-0.062	0.035	-0.004	0.003	-0.002	0.001
Ph	0.102	0.148	0.856	0.467	0.003	0.011	-0.011	0.009
Ph^2	-0.103	0.087	-0.158	0.242	-0.006	0.007	-0.002	0.005
Biotic condition								
Fi	**0.795**	**0.229**	**2.028**	**0.591**	-0.307	0.336	**0.327**	**0.151**
Pr	**0.161**	**0.059**	-0.031	0.055	-0.085	0.139	**0.085**	**0.022**
Pbb			**0.099**	**0.044**	**1.568**	**0.318**	0.022	0.032
Pbv	0.064	0.144			-1.046	0.608	-0.071	0.056
Pte	**0.514**	**0.121**	-0.052	0.064			**0.184**	**0.036**
Pla	0.205	0.118	0.066	0.065	**2.048**	**0.365**		
Probability of detection								
Intercept	**0.455**	**0.078**	**-1.238**	**0.140**	**1.307**	**0.145**	**1.263**	**0.083**
YY	**-0.458**	**0.097**			**-1.102**	**0.128**	**-1.050**	**0.095**
D	**0.914**	**0.076**	**2.537**	**0.294**	**-0.682**	**0.088**	**-1.114**	**0.063**
D^2	**-1.547**	**0.084**	**-1.239**	**0.187**	**-1.436**	**0.103**	**-1.009**	**0.065**
Ar					**-0.235**	**0.069**		
Ar^2								
Si					**-0.367**	**0.125**		

Note: Factors with bold values do not include zero in 95% confidence intervals.

B. b. spinosus and *R. latastei* most likely occurred in ponds where the risk of potentially predatory encounters was high (Fig. 1F). The occurrence of *B. viridis* and *R. temporaria* in turn was marginally affected by predation risk (i.e. confidence intervals included zero; Table 4), an index including the abundance of predators excluding fish, but see Table 1. The presence of potentially competitive fishes (length ≥ 10 cm) positively affected the occurrence of all species, except of *R. temporaria* (Fig. 1G). Species did not avoid ponds that were occupied by other species. In fact, the presence of other species had positive effects on occurrence (Table 4). This was true for the three early-breeding species *R. temporaria*, *R. latastei*, and *B. b. spinosus*. The two frog species were rarely found in ponds with *B. viridis*. Frogs and *B. b. spinosus* breed early in the season when *B. viridis* is absent at breeding sites. Hence, the low proportion of shared ponds of all four species was rather due to the late breeding period of *B. viridis* than competition avoidance.

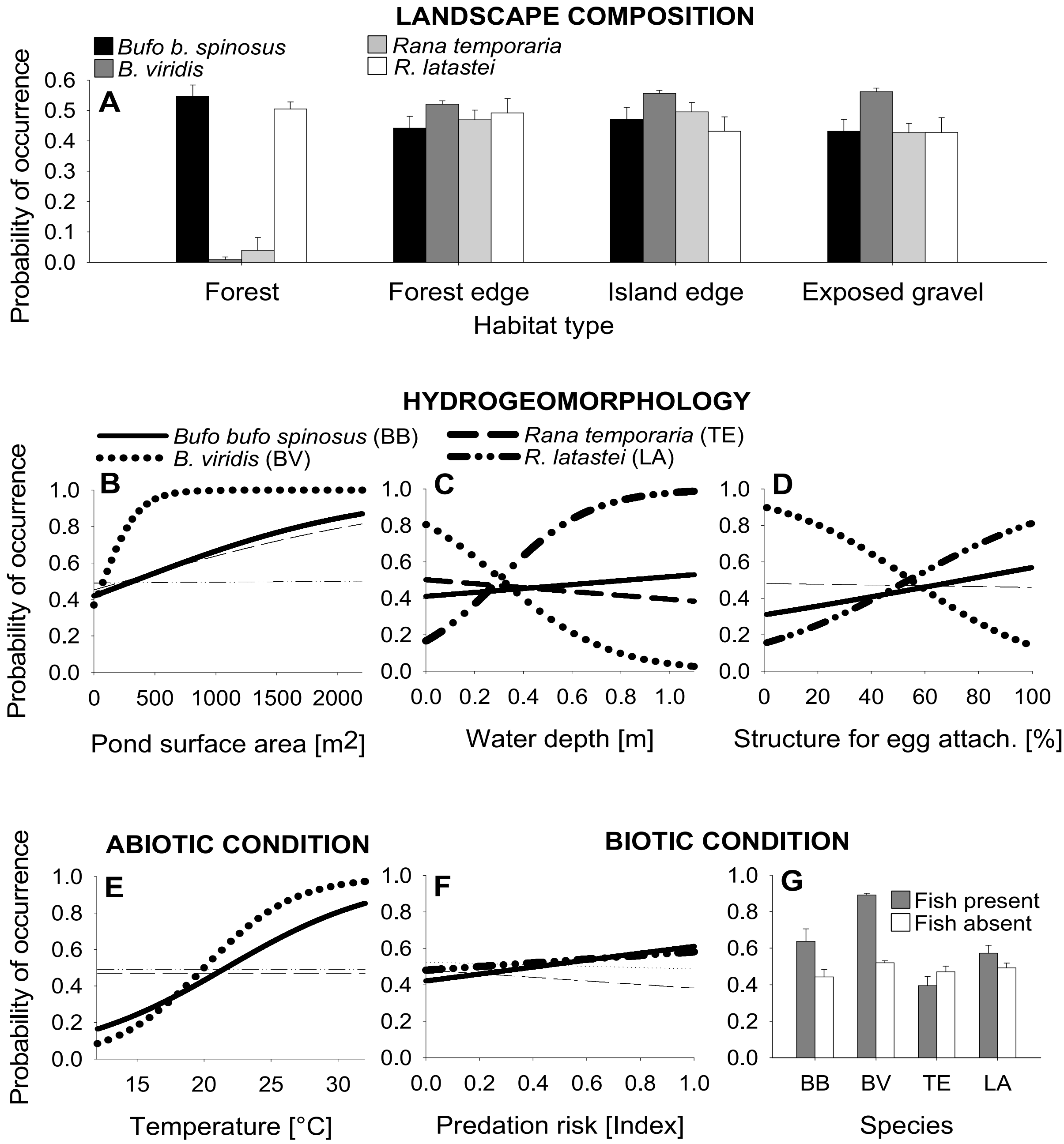


Figure 1: Predicted probability of occurrence for four factor groups: (A) landscape composition, (B-D) hydrogeomorphology, (E) abiotic condition, and (F-G) biotic condition. Thick lines denote significant relationships (i.e. regression slopes did not include zero in confidence intervals). Vertical lines in histograms are upper 95% confidence intervals.

The comparison of species pairs showed that preferences of species differed in relation to abiotic and/or biotic factors (Table 5). One factor was the availability of structural elements for egg attachment such as twigs and branches

(Table 5, Fig. 1D). *B. b. spinosus* and *Rana latastei* selected breeding sites where the availability of structural elements for egg attachment was high while *B. viridis* avoided them. *B. b. spinosus* and *R. temporaria* were separated by different responses to temperature, presence of fish, and predation risk. The factors that separated *B. b. spinosus* and *R. latastei* in breeding site selection were temperature and water depth (Table 5, Fig. 1C,E). The occurrence of *B. b. spinosus* was highest in warm ponds independent of pond size (Appendix F). The occurrence of *R. latastei* in turn was highest in cool and deep ponds (Appendix F). The factors that separated the two frog species in breeding site selection were water depth, the presence of fish, and predation risk (Tables 4 and 5, Fig. 1). *Bufo viridis* and the two frog species were separated seasonally. In addition, *B. viridis* prefered breeding sites where fishes were present while *R. temporaria* avoided them. And, *B. viridis* prefered warm and shallow ponds without structural elements for egg attachment, and low predation risk, while *R. latastei* most frequently occurred in ponds with opposite characteristics.

Table 5. Comparison of species pairs in relation to factors for which species differed in their response, i.e. while breeding site selection of one species was positively related to a specific factor, breeding site selection of the other species was negatively related to the same factor.

	Bufo b. spinosus	*B. viridis*	*Rana latastei*	*R. temporaria*
Bufo b. spinosus	.	St, De, Pr*	T*, De*	T*, Fi*, Pr*
B. viridis		.	St, De, T*, Pr*, seasonal	Fi*, seasonal
Rana latastei			.	De*, Fi*, Pr*
R. temporaria				.

Note: Comparisons are based on Table 4. See Table 1 for abbreviations of factors.

* for one of the two species, the factor included zero in 95% confidence intervals.

Discussion

Our results demonstrate that the joint effects of the abiotic and biotic environment govern local breeding site selection of anurans in a dynamic floodplain. All species used habitat types similarly, with the exception that two species avoided one out of four habitat types (Fig. 1). Within habitat types, species selected breeding ponds based on different ecological factors (Fig. 1). Species did not avoid each other; in contrast, high rates of co-occurrence as well as statistical parameter estimates showed that species preferred ponds that were occupied by other anuran species and fish (Table 4, Fig. 1G). Our results therefore indicate that both differential habitat type preferences and ecological segregation along environmental gradients permit co-existence in the larval anuran community at the pond-level. Competitor avoidance currently appears to play a minor role in breeding site selection and hence local co-existence. Our main result is that "life attracts life", which indicates that characteristics of the favourable ponds covary among anurans and fish.

Patterns of occurrence

We propose two explanations for the high rates of species co-occurrence, and the lack of support for competition observed: i) seasonal segregation, and ii) niche differentiation along general environmental gradients in habitat quality. Our results strongly support niche differentiation, but not seasonal segregation:

The rate of co-occurrence of *B. b. spinsous* with frogs (*R. temporaria, R. latastei*) was 17.3% and with *B. viridis* 12.4%, and all species co-occurred in 1.5% of ponds. Hence, rates of co-occurrence were higher than expected by chance (Appendix G). The parameter estimates indicated that frogs avoid *B. viridis* (Table 4). However, *B. viridis* was not yet breeding and therefore absent from the ponds when frogs selected breeding sites (L. Indermaur, *personal observation*). In fact, species with overlapping breeding periods (Appendix E: *B.*

b.spinosus with frogs, *B. b. spinosus* with *B. viridis*), preferably colonized ponds that were occupied by other species (Table 4). Seasonal segregation is therefore unlikely to facilitate co-existence in anurans (Alford and Wilbur 1985; Lawler and Morin 1993; Vignoli et al. 2007).

ii) All species largely preferred similar habitat types (Fig. 1A). Preference of similar habitat types probably stems from large variation among habitat types in larval productivity that is experienced in a similar way by all species. In other words, some ponds tend to be "good" environments for all species, including not only anurans but also fish, and remain productive to a degree that outweighed the possible negative effects of increased interspecific interactions. We therefore predicted local species diversity of anurans to identify the habitat characteristics that may constitute diverse fresh water communities. Local anuran diversity was highest in large, warm, deep as well as structurally complex ponds (Appendix H), thereby largely corroborating classical expectations (Connell and Orias 1964; Macarthur and Macarthur 1961; Pianka 1967). However, local species diversity decreased far from environmental optima, suggesting that the abiotic environment constrains the distribution and diversity of freshwater communities.

When examined in detail, the species selected breeding sites differently in relation to abiotic and biotic factors (Tables 4 and 5, Fig. 1). Our results therefore support the view that co-existence is facilitated through some degree of niche-differentiation along environmental gradients, constituting similar findings by earlier studies (Richter-Boix et al. 2007; Van Buskirk 2003; Van Buskirk 2005). However, our results (Table 4) join other results (Van Buskirk 2007) that do not support the role of competition, thereby contrasting with the classical expectations (Gause 1934; Hardin 1960) and empirical studies (Bardsley and Beebee 2001; Hairston 1980; Laurila 2000; Petranka et al. 1994; Resetarits and Wilbur 1989; Wilbur and Alford 1985). In a previous study where high species diversity in the dynamic floodplain was studied, the authors ascribed the high species diversity observed to the typically high structural organization of unpredictable environments (Tockner et al. 2006). The evolution of habitat preferences that allow high species diversity is therefore likely associated with the distribution of habitats, environmental gradients, and the disturbances that maintain these gradients (Tilman 2004).

In this study we identified the factors governing breeding site selection of individual species. In the following, we discuss differential habitat preferences in more detail to shed light on differences in the species' tolerance to limiting factors. All species selected breeding sites in relation to water depth, which is a surrogate for hydroperiod (Fig. 1C). Species, however, preferred either deep or shallow ponds, which re-emphasizes the importance of gradients in hydroperiod for the distribution and composition of freshwater communities (Van Buskirk 2003; Van Buskirk 2005; Wellborn et al. 1996).

Toads preferably used warm and large ponds, while frogs selected ponds independent of temperature and the size of ponds (Table 4, Fig. 1 B,E, Appendix F). This implies that toads are absent from small and cold ponds, which was not true for our and other studies (Knutson et al. 2004; Laurila 1998). The selection of large and warm ponds by toads is rather linked to larval performance. Indeed, larvae of *B. b. spinosus* quickly grew to a large size at metamorphosis in warm and large ponds that were characteristic for the active tract (Indermaur et al. 2008a). In ponds of the riparian forest in turn, *B. b. spinosus* slowly grew to small metamorphic size. Moreover, production of metamorphs was about one to two orders of magnitude smaller in the riparian forest than in the active tract (Indermaur et al. 2008a). This implies that larger ponds are more productive than small ponds, and that higher temperatures are needed to process food, and hence promote growth of toad larvae. Furthermore, the habitat type specific growth rates observed (Indermaur et al. 2008a) emphasize the potential impacts of habitat selection on population dynamics (Werner et al. 1983).

Water depth and predation risk were the two main factors that separated all four species in breeding site selection and probably facilitate their co-existence (Tables 4 and 5, Fig. 1). For example, the toad *B. viridis* and the frog *R. temporaria* most likely occurred in low-predation risk ponds, which because of frequent drying and flooding, are typical for the active tract (Table 2, Fig. 1A). The toad *B. b. spinosus* and the frog *R. latastei* most likely occurred in high predation risk ponds that were characteristic for the riparian forest (Table 2, Fig. 1A). Intuitively, we would expect that prey species avoid predation risk (Resetarits 2001; Resetarits and Wilbur 1989; Rieger et al. 2004) but positive correlation between predator and prey density may occur (Van Buskirk and Schmidt 2000). Furthermore, adult amphibians are known to perceive the presence of predators that consume their larvae (Rieger et al. 2004; Spieler and Linsenmair 1997). The usually higher productivity in high-predation risk environments may have outweighed negative effects of predation (Reznick et al. 2000). However, this is unlikely, as ponds in the active tract were warmer and more productive than ponds in the riparian forest (Table 2, but see Indermaur et al. 2008a for productivity): The selection of high-predation risk ponds rather suggests a positive feedback between predation risk and larval performance (Indermaur et al. 2008a; Reznick et al. 2001). The expectation is that high predator densities reduce intraspecific competition. Thereby resource availability increases, which improves growth conditions for remaining individuals (Peacor 2002).

Conclusions and conservation implications

We clarified the role of the abiotic environment, predation risk, and competition on breeding site selection of a diverse anuran community in a dynamic pristine floodplain. Our results demonstrate that both differential habitat type preferences and ecological segregation along environmental gradients permit temporal co-existence within ponds in the larval anuran community studied (Alford and Wilbur 1985; Lawler and Morin 1993; Vignoli et al. 2007). Hence, local species diversity is governed by variation in abiotic and biotic conditions to which species differentially respond. Our results do not support the pervasive role of competition in governing breeding site selection and hence co-existence. Unpredictable ecosystems seem to be highly structured in habitat quality, which is frequently reset by disturbance (Gallet et al. 2007). Covariance in habitat preference along environmental gradients among species seemed to outweigh the importance of competition avoidance and may explain the high species diversity in the unpredictable environments observed. This result is similar to our study on terrestrial habitat selection of toads (Indermaur et al. 2008b), suggesting that differential habitat preferences are evident in all life history stages of species with complex life cycles. Local co-existence follows from individuals of each species being able to recognize the best habitat types for their tadpoles.

Other studies predicted regional species diversity accurately assuming neutral processes (Hubbell 2001; Muneepeerakul et al. 2008; Tilman 2004). Based on our results we can clearly reject the neutral model, as most species combinations were found locally co-existing in higher frequency than expected by chance (Appendix G). Regional diversity summarizes processes affecting local diversity and may not be very informative when factors determining co-existence are studied. Our results therefore emphasize that for management planning it is very important to identify the features that make ponds attractive for multiple species. Ponds that constitute locally diverse freshwater communities are of intermediate size, depth, temperature, and structural complexity (Appendix H). Hence, species diversity decreases far from environmental optima, suggesting that the abiotic environment constrains the distribution and diversity of freshwater communities.

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Appendix A. Correlationmatrix of factors used in candidate models for predicting the probability of occurrence.

Code	Factor	Ar	De	St	Hp	Sh	T	Al	Ox	Ph	Cy	Pr	Ebb	Ebv	Ete	Ela
Ar	Pond surface area	1.000	0.290	-0.140	0.160	-0.180	-0.060	0.360	0.070	0.070	0.090	0.020	-0.110	-0.040	-0.070	-0.070
De	Water depth		1.000	0.310	0.400	0.120	-0.140	0.350	-0.060	-0.080	-0.040	0.010	-0.100	-0.120	-0.060	0.040
St	Structural elements for egg attachment			1.000	0.270	0.480	-0.190	0.150	-0.100	-0.170	-0.120	0.040	0.140	-0.190	0.010	0.110
Hp	Hydroperiod length				1.000	0.210	-0.180	0.310	0.020	-0.050	-0.080	0.050	-0.090	-0.130	0.060	0.100
Sh	Shading					1.000	-0.270	-0.090	-0.180	-0.170	-0.360	0.090	0.160	-0.180	0.060	0.140
T	Temperature						1.000	-0.040	0.160	0.340	-0.010	0.040	0.130	0.250	-0.040	-0.130
Al	Algae cover							1.000	0.320	0.270	0.050	-0.020	-0.050	-0.010	-0.090	-0.060
Ox	Oxygen concentration								1.000	0.630	0.150	0.060	-0.100	0.090	-0.130	-0.080
Ph	Ph									1.000	-0.060	0.090	0.040	0.150	-0.050	-0.090
Cy	Specific conductance										1.000	-0.120	-0.090	0.000	-0.130	-0.080
Pr	Predation risk											1.000	-0.010	-0.020	<0.001	-0.010
Ebb	Egg density *B. b. spinosus*												1.000	0.010	0.030	<0.001
Ebv	Egg density *B.viridis*													1.000	-0.050	-0.050
Ete	Egg density *Rana temporaria*														1.000	0.130
Ela	Egg density *R. latastei*															1.000

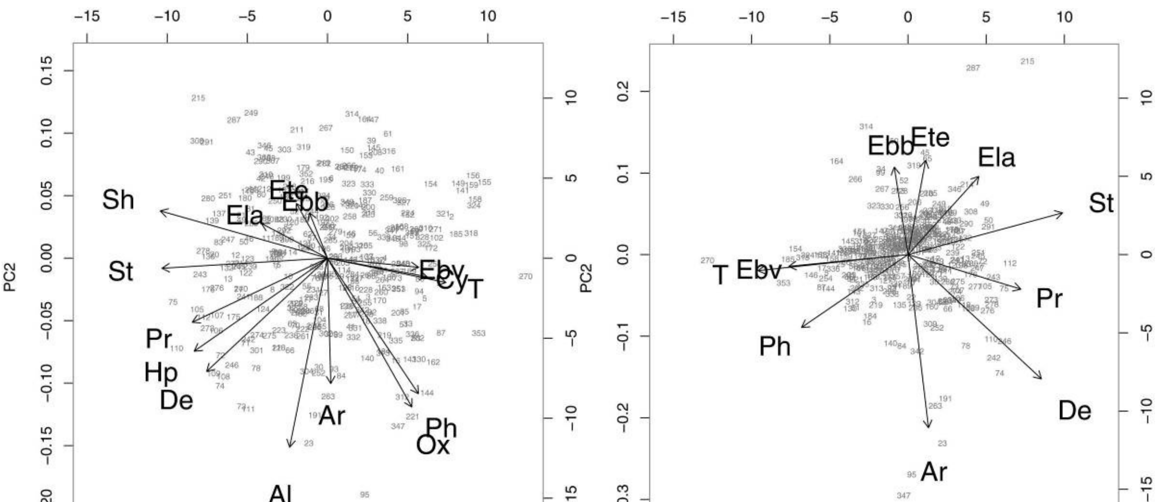
Note: See Table 1 for abbreviations of factors. All factors were standardized prior to calculating Pearson coefficients.

Appendix B. Results from a principal component analysis for the full set of measured factors (A), and the set of factors that were selected for modelling the probability of occurrence (B). See Table 1 for abbreviations of factors.

Figure A) shows that predation (Pr), hydroperiod length (Hp), and water depth (De) describe similar pond characteristics. Similarly, algae cover (Al) and pond surface area (Ar) or pH and oxygen concentration or specific conductance (Cy), temperature (T), and egg clutch density of *Bufo viridis* (Ebv), describe similar pond characteristics. The grouping among the remaining factors shading (Sh), structural elements for egg attachment (St) and egg clutch densities of *Rana latastei* (Ela), *R. temporaria* (Ete), and *B. viridis* (Ebb) is less pronounced.

Figure B) shows no distinct grouping among factors. Hence, factors characterize different characteristics of ponds. Except, temperature (T) and egg clutch densities of *Bufo viridis* describe similar pond characteristics.

A) B)



Appendix C. Model selection results for predicting the probability of detection (p), sorted after differences between Akaike's small sample information criterion (ΔQAICc), corrected for overdispersion with the variance inflation factor ($\hat{c}$).

Model no.	Factors						K	ΔQAICc	Qweight	Qdeviance
Bufo b. spinosus: ψ = (.), $\hat{c}$= 4.75										
10	YY	Day	Day^2				5	0.00	0.431	653.19
11	YY	Day	Day^2			Si	6	1.92	0.165	653.04
12	YY	Day	Day^2	Ar			6	2.05	0.155	653.17
5		Day	Day^2				4	2.74	0.110	657.99
14	YY	Day	Day^2	Ar	Ar^2		7	3.98	0.059	653.02
13	YY	Day	Day^2	Ar		Si	7	3.99	0.059	653.03
15	YY	Day	Day^2	Ar	Ar^2	Si	8	5.91	0.022	652.85
9	YY	Day					4	121.37	0.000	776.62
4		Day					3	122.83	0.000	780.12
2							3	128.74	0.000	786.03
8	YY					Si	4	130.67	0.000	785.92
1	(.)						2	131.81	0.000	444.98
3						Si	3	133.83	0.000	791.13
6				Ar			3	133.85	0.000	791.14
7				Ar	Ar^2		4	135.87	0.000	791.12
B. viridis: ψ = (.), $\hat{c}$ = 3.84										
5		Day	Day^2				4	0.00	0.452	235.16
10	YY	Day	Day^2				5	1.66	0.197	234.76
11	YY	Day	Day^2			Si	6	2.97	0.102	234.00
14	YY	Day	Day^2	Ar	Ar^2		7	3.14	0.094	232.10
12	YY	Day	Day^2	Ar			6	3.71	0.071	234.75
15	YY	Day	Day^2	Ar	Ar^2	Si	8	4.51	0.047	231.37
13	YY	Day	Day^2	Ar		Si	7	5.03	0.036	233.99
4		Day					3	14.67	0.000	251.88
9	YY	Day					4	16.54	0.000	251.71
1	(.)						2	49.40	0.000	139.79
2							3	50.25	0.000	287.46
3						Si	3	50.87	0.000	288.08
8	YY					Si	4	51.01	0.000	286.17
6				Ar			3	51.42	0.000	288.63
7				Ar	Ar^2		4	51.96	0.000	287.13
Rana temporaria: ψ = (.), $\hat{c}$ = 1.79										
13	YY	Day	Day^2	Ar		Si	7	0.00	0.489	1146.40
15	YY	Day	Day^2	Ar	Ar^2	Si	8	1.11	0.280	1145.41
12	YY	Day	Day^2	Ar			6	2.75	0.124	1151.23
14	YY	Day	Day^2	Ar	Ar^2		7	4.57	0.050	1150.97
11	YY	Day	Day^2			Si	6	5.00	0.040	1153.48
10	YY	Day	Day^2				5	6.76	0.017	1157.31

5		Day	Day^2				4	43.14	0.000	1195.74
9	YY	Day					4	181.32	0.000	1333.93
8	YY					Si	4	209.41	0.000	1362.02
2							3	210.40	0.000	1365.05
4		Day					3	216.46	0.000	1371.12
6				Ar			3	234.64	0.000	1389.29
7				Ar	Ar^2		4	236.65	0.000	1389.26
1	(.)						2	237.00	0.000	806.53
3						Si	3	238.65	0.000	1393.31
R. latastei: ψ = (.), $\hat{c}$ = 9.24										
10	YY	Day	Day^2				5	0.00	0.394	353.56
12	YY	Day	Day^2	Ar			6	1.25	0.211	352.74
11	YY	Day	Day^2			Si	6	1.60	0.177	353.09
13	YY	Day	Day^2	Ar		Si	7	2.66	0.104	352.07
14	YY	Day	Day^2	Ar	Ar^2		7	3.29	0.076	352.69
15	YY	Day	Day^2	Ar	Ar^2	Si	8	4.68	0.038	351.99
5		Day	Day^2				4	11.77	0.001	367.38
9	YY	Day					4	32.36	0.000	387.97
4		Day					3	44.88	0.000	402.54
2							3	76.24	0.000	433.90
8	YY					Si	4	77.94	0.000	433.55
1	(.)						2	81.72	0.000	283.54
6				Ar			3	83.12	0.000	440.78
3						Si	3	83.56	0.000	441.22
7				Ar	Ar^2		4	85.16	0.000	440.78

Note: See Table 1 for abbreviations of factors. (.) = constant probability of occurrence (ψ). The top ranked model with ΔQAICc = 0 best approximates the data and models with ΔQAICc ≤ 2 are considered to receive substantial support from the data. Number of factors (K) and Akaike weights are given. When one model receives weights ≥ 0.9 there is no model selection uncertainty apparent. Factor year was included in every model to correct for its potential impact. All factors were modelled as additive effects.

Appendix D. Model selection results for predicting the probability of occurrence (ψ), sorted after differences between Akaike's small sample information criterion (ΔQAICc), corrected for overdispersion with the variance inflation factor ($\hat{c}$).

Model selection results for *Bufo b. spinosus* ($\hat{c}$= 5.51)

Model no.	Factors															K	ΔQAICc	Qweight	Qdeviance
Single factor groups																			
56							T	T^2	Ph	Ph^2						10	2.39	0.045	560.75
58											Fi	Pr	Pbv	Pte	Pla	11	5.23	0.011	555.43
45							T		Ph	Ph^2						9	5.36	0.010	558.29
57											Fi					7	7.24	0.004	563.33
1																6	7.48	0.004	561.02
23		Ar		De		St										9	8.68	0.002	554.97
34		Ar	Ar^2	De	De^2	St										11	10.05	0.001	550.61
12	Ht															9	11.14	0.001	549.89
Sum																		0.078	
Multiple factor groups, linear																			
9							T		Ph	Ph^2		Pr	Pbv	Pte	Pla	14	1.36	0.076	540.31
5		Ar		De		St	T		Ph	Ph^2						12	1.55	0.069	544.81
16		Ar		De		St	T		Ph	Ph^2	Fi					13	2.20	0.050	543.31
17		Ar		De		St	T		Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	17	4.40	0.017	536.81
14	Ht						T		Ph	Ph^2	Fi					13	4.50	0.016	545.61
8							T		Ph	Ph^2	Fi					10	4.67	0.015	552.17
10	Ht	Ar		De		St	T		Ph	Ph^2						15	6.21	0.007	543.00
18	Ht	Ar		De		St	T		Ph	Ph^2	Fi					16	6.22	0.007	540.82
15	Ht						T		Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	17	6.25	0.007	538.66
2	Ht						T		Ph	Ph^2						12	6.71	0.005	549.96
7		Ar		De		St					Fi	Pr	Pbv	Pte	Pla	14	9.21	0.001	548.16
6		Ar		De		St					Fi					10	9.41	0.001	556.91
4	Ht										Fi	Pr	Pbv	Pte	Pla	14	9.45	0.001	548.40
3	Ht										Fi					10	10.07	0.001	557.58
19	Ht	Ar		De		St	T		Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	20	10.20	0.001	535.94
59	Ht	Ar		De		St										12	13.70	0.000	556.95
11	Ht	Ar		De		St					Fi					13	14.04	0.000	555.15
13	Ht	Ar		De		St					Fi	Pr	Pbv	Pte	Pla	17	14.20	0.000	546.61
Sum																		0.274	
Multiple factor groups, quadratic																			
32							T	T^2	Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	15	0.00	0.150	536.79
26		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2						15	1.02	0.090	537.80
31							T	T^2	Ph	Ph^2	Fi					11	1.48	0.072	546.86
41	Ht						T	T^2	Ph	Ph^2	Fi					14	1.63	0.066	540.59
46		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi					16	2.06	0.053	536.67
24		Ar	Ar^2	De		St	T		Ph	Ph^2						13	2.27	0.048	543.38
25		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2						14	2.83	0.036	541.78
43		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi					14	3.36	0.028	542.32
44		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi					15	3.98	0.020	540.77
22	Ht						T	T^2	Ph	Ph^2						13	4.11	0.019	545.22
42	Ht						T	T^2	Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	18	4.65	0.015	534.85
36	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2						18	5.59	0.009	535.80
52	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi					19	6.05	0.007	534.03

47		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	18	6.22	0.007	536.42
49		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	20	6.44	0.006	532.19
33	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2						16	6.75	0.005	541.35
50	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi					17	7.35	0.004	539.76
35	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2						17	7.49	0.004	539.90
48		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	19	7.86	0.003	535.84
51	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi					18	8.16	0.003	538.36
27		Ar	Ar^2	De		St					Fi					11	10.20	0.001	555.58
29		Ar	Ar^2	De		St					Fi	Pr	Pbv	Pte	Pla	15	10.88	0.001	547.67
28		Ar	Ar^2	De	De^2	St					Fi					12	11.37	0.001	554.63
53	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	21	11.92	0.000	535.42
55	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	23	11.98	0.000	530.94
30		Ar	Ar^2	De	De^2	St					Fi	Pr	Pbv	Pte	Pla	16	12.81	0.000	547.42
54	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi	Pr	Pbv	Pte	Pla	22	13.63	0.000	534.87
20	Ht	Ar	Ar^2	De		St										13	13.69	0.000	554.80
37	Ht	Ar	Ar^2	De		St					Fi					14	14.61	0.000	553.56
21	Ht	Ar	Ar^2	De	De^2	St										14	14.82	0.000	553.77
39	Ht	Ar	Ar^2	De		St					Fi	Pr	Pbv	Pte	Pla	18	15.80	0.000	546.00
38	Ht	Ar	Ar^2	De	De^2	St					Fi					15	15.86	0.000	552.64
40	Ht	Ar	Ar^2	De	De^2	St					Fi	Pr	Pbv	Pte	Pla	19	17.83	0.000	545.81
Sum																		0.649	
Total																		1.000	

Note: See Table 1 for abbreviations of factors. Model no. 1 = constant probability of occurrence (ψ). The top ranked model with ΔQAICc = 0 best approximates the data and models with ΔQAICc ≤ 2 are considered to receive substantial support from the data. Number of factors (K) and Akaike weights are given. When one model receives weights ≥ 0.9 there is no model selection uncertainty apparent. Factor year was included in every model to correct for its potential impact. Factor year was included in every model to correct for its potential impact.

Model selection results for *B. viridis* ($\hat{c}$ = 1.41)

Model no.	Factors															K	ΔQAICc	Qweight	Qdeviance
Single factor groups																			
34		Ar	Ar^2	De	De^2	St										10	31.81	0.000	575.84
23		Ar		De		St										8	32.72	0.000	580.95
12	Ht															8	51.34	0.000	599.57
45							T		Ph	Ph^2						8	52.54	0.000	600.77
56							T	T^2	Ph	Ph^2						9	54.26	0.000	600.39
58											Fi	Pr	Pbb	Pte	Pla	10	55.43	0.000	599.46
1																5	84.56	0.000	639.00
57											Fi					6	78.98	0.000	631.36
Sum																		0.000	
Multiple factor groups, linear																			
16		Ar		De		St	T		Ph	Ph^2	Fi					12	0.00	0.279	539.78
18	Ht	Ar		De		St	T		Ph	Ph^2	Fi					15	3.60	0.046	536.92
17		Ar		De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	16	4.30	0.032	535.43
19	Ht	Ar		De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	19	7.25	0.007	531.75
5		Ar		De		St	T		Ph	Ph^2						11	8.49	0.004	550.40
10	Ht	Ar		De		St	T		Ph	Ph^2						14	10.52	0.001	546.00
13	Ht	Ar		De		St					Fi	Pr	Pbb	Pte	Pla	16	20.10	0.000	551.23
7		Ar		De		St					Fi	Pr	Pbb	Pte	Pla	13	20.83	0.000	558.47
11	Ht	Ar		De		St					Fi					12	23.69	0.000	563.47
6		Ar		De		St					Fi					9	26.13	0.000	572.26
59	Ht	Ar		De		St										11	28.52	0.000	570.43
15	Ht						T		Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	16	31.21	0.000	562.34
14	Ht						T		Ph	Ph^2	Fi					12	31.35	0.000	571.13
2	Ht						T		Ph	Ph^2						11	35.78	0.000	577.69
9							T		Ph	Ph^2		Pr	Pbb	Pte	Pla	13	36.42	0.000	574.06
4	Ht										Fi	Pr	Pbb	Pte	Pla	13	45.18	0.000	582.82
8							T		Ph	Ph^2	Fi					9	45.41	0.000	591.55
3	Ht										Fi					9	49.10	0.000	595.23
Sum																		0.370	
Multiple factor groups, quadratic																			
43		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi					13	0.01	0.278	537.64
46		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi					15	1.78	0.115	535.09
44		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi					14	2.16	0.095	537.64
50	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi					16	3.04	0.061	534.17
51	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi					17	5.23	0.020	534.16
52	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi					18	5.26	0.020	531.99
47		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	17	6.36	0.012	535.30
24		Ar	Ar^2	De		St	T		Ph	Ph^2						12	6.86	0.009	546.64
49		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	19	8.03	0.005	532.54
48		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	18	8.32	0.004	535.05
33	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2						15	8.51	0.004	541.82
53	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	20	9.36	0.003	531.63
35	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2						16	10.65	0.001	541.78
54	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	21	11.57	0.001	531.60
36	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2						17	11.84	0.001	540.78
55	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	22	11.95	0.001	529.71
25		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2						13	12.12	0.001	549.76
26		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2						14	12.92	0.000	548.40
37	Ht	Ar	Ar^2	De		St					Fi					13	21.84	0.000	559.47

39	Ht	Ar	Ar^2	De		St					Fi	Pr	Pbb	Pte	Pla	17	22.27	0.000	551.20
29		Ar	Ar^2	De		St					Fi	Pr	Pbb	Pte	Pla	14	22.98	0.000	558.46
38	Ht	Ar	Ar^2	De	De^2	St					Fi					14	23.98	0.000	559.46
40	Ht	Ar	Ar^2	De	De^2	St					Fi	Pr	Pbb	Pte	Pla	18	24.42	0.000	551.15
27		Ar	Ar^2	De		St					Fi					10	24.93	0.000	568.96
30		Ar	Ar^2	De	De^2	St					Fi	Pr	Pbb	Pte	Pla	15	25.15	0.000	558.46
20	Ht	Ar	Ar^2	De		St										12	25.26	0.000	565.04
28		Ar	Ar^2	De	De^2	St					Fi					11	26.91	0.000	568.82
21	Ht	Ar	Ar^2	De	De^2	St										13	27.40	0.000	565.04
42	Ht						T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	17	32.72	0.000	561.66
41	Ht						T	T^2	Ph	Ph^2	Fi					13	33.21	0.000	570.85
32							T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pte	Pla	14	36.92	0.000	572.40
22	Ht						T	T^2	Ph	Ph^2						12	37.63	0.000	577.41
31							T	T^2	Ph	Ph^2	Fi					10	47.12	0.000	591.15
Sum																		0.630	
Total																		1.000	

Note: See Table 1 for abbreviations of factors. Model no. 1 = constant probability of occurrence (ψ). The top ranked model with ΔQAICc = 0 best approximates the data and models with ΔQAICc ≤ 2 are considered to receive substantial support from the data. Number of factors (*K*) and Akaike weights are given. When one model receives weights ≥ 0.9 there is no model selection uncertainty apparent. Factor year was included in every model to correct for its potential impact. Factor year was included in every model to correct for its potential impact.

Model selection results for *Rana temporaria* ($\hat{c}$ = 1.68)

Model no.	Factors															K	ΔQAICc	Qweight	Qdeviance
Single factor groups																			
58											Fi	Pr	Pbb	Pbv	Pla	13	0.00	0.487	1164.57
34		Ar	Ar^2	De	De^2	St										13	27.05	0.000	1191.62
12	Ht															11	36.29	0.000	1205.13
23		Ar		De		St										11	37.75	0.000	1206.60
56							T	T^2	Ph	Ph^2						12	42.21	0.000	1208.92
1																8	46.46	0.000	1221.63
57											Fi					9	46.48	0.000	1219.54
45							T		Ph	Ph^2						11	50.66	0.000	1219.50
Sum																		0.487	
Multiple factor groups, linear																			
7		Ar		De		St					Fi	Pr	Pbb	Pbv	Pla	16	2.77	0.122	1160.84
4	Ht										Fi	Pr	Pbb	Pbv	Pla	16	3.06	0.106	1161.12
13	Ht	Ar		De		St					Fi	Pr	Pbb	Pbv	Pla	19	4.61	0.049	1156.05
9							T		Ph	Ph^2		Pr	Pbb	Pbv	Pla	16	6.22	0.022	1164.28
17		Ar		De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	19	8.81	0.006	1160.25
15	Ht						T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	19	9.48	0.004	1160.92
19	Ht	Ar		De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	22	11.01	0.002	1155.71
3	Ht										Fi					12	33.97	0.000	1200.68
59	Ht	Ar		De		St										14	34.93	0.000	1197.35
11	Ht	Ar		De		St					Fi					15	35.15	0.000	1195.39
14	Ht						T		Ph	Ph^2	Fi					15	37.01	0.000	1197.25
10	Ht	Ar		De		St	T		Ph	Ph^2						17	37.16	0.000	1193.03
18	Ht	Ar		De		St	T		Ph	Ph^2	Fi					18	37.48	0.000	1191.14
2	Ht						T		Ph	Ph^2						14	39.16	0.000	1201.57
6		Ar		De		St					Fi					12	39.17	0.000	1205.88
5		Ar		De		St	T		Ph	Ph^2						14	41.49	0.000	1203.91
16		Ar		De		St	T		Ph	Ph^2	Fi					15	42.99	0.000	1203.23
8							T		Ph	Ph^2	Fi					12	50.69	0.000	1217.40
Sum																		0.310	
Multiple factor groups, quadratic																			
30		Ar	Ar^2	De	De^2	St					Fi	Pr	Pbb	Pbv	Pla	18	3.72	0.076	1157.38
29		Ar	Ar^2	De		St					Fi	Pr	Pbb	Pbv	Pla	17	4.84	0.043	1160.71
40	Ht	Ar	Ar^2	De	De^2	St					Fi	Pr	Pbb	Pbv	Pla	21	5.35	0.033	1152.31
39	Ht	Ar	Ar^2	De		St					Fi	Pr	Pbb	Pbv	Pla	20	6.61	0.018	1155.82
32							T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	17	6.72	0.017	1162.59
48		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	21	9.57	0.004	1156.52
49		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	22	9.81	0.004	1154.50
42	Ht						T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	20	10.13	0.003	1159.33
47		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	20	10.92	0.002	1160.12
54	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	24	11.65	0.001	1151.79
55	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	25	11.90	0.001	1149.73
53	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pla	23	13.05	0.001	1155.47
36	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2						20	19.71	0.000	1168.91
52	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi					21	20.93	0.000	1167.88
21	Ht	Ar	Ar^2	De	De^2	St										16	22.88	0.000	1180.94
38	Ht	Ar	Ar^2	De	De^2	St					Fi					17	23.89	0.000	1179.76
26		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2						17	24.04	0.000	1179.91
35	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2						19	24.08	0.000	1175.52
51	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi					20	25.23	0.000	1174.43

46		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	18	25.97	0.000	1179.63
28		Ar	Ar^2	De	De^2	St					Fi	14	28.90	0.000	1191.31
25		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2		16	30.05	0.000	1188.11
41	Ht						T	T^2	Ph	Ph^2	Fi	16	31.24	0.000	1189.30
44		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi	17	31.95	0.000	1187.82
22	Ht						T	T^2	Ph	Ph^2		15	32.66	0.000	1192.90
20	Ht	Ar	Ar^2	De		St						15	35.80	0.000	1196.05
37	Ht	Ar	Ar^2	De		St					Fi	16	36.46	0.000	1194.52
33	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2		18	38.42	0.000	1192.08
50	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	19	39.10	0.000	1190.54
27		Ar	Ar^2	De		St					Fi	13	40.51	0.000	1205.08
31							T	T^2	Ph	Ph^2	Fi	13	42.69	0.000	1207.26
24		Ar	Ar^2	De		St	T		Ph	Ph^2		15	42.77	0.000	1203.02
43		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	16	44.49	0.000	1202.55
Sum														0.204	
Total														1.000	

Note: See Table 1 for abbreviations of factors. Model no. 1 = constant probability of occurrence (ψ). The top ranked model with ΔQAICc = 0 best approximates the data and models with ΔQAICc ≤ 2 are considered to receive substantial support from the data. Number of factors (*K*) and Akaike weights are given. When one model receives weights ≥ 0.9 there is no model selection uncertainty apparent. Factor year was included in every model to correct for its potential impact. Factor year was included in every model to correct for its
potential impact.

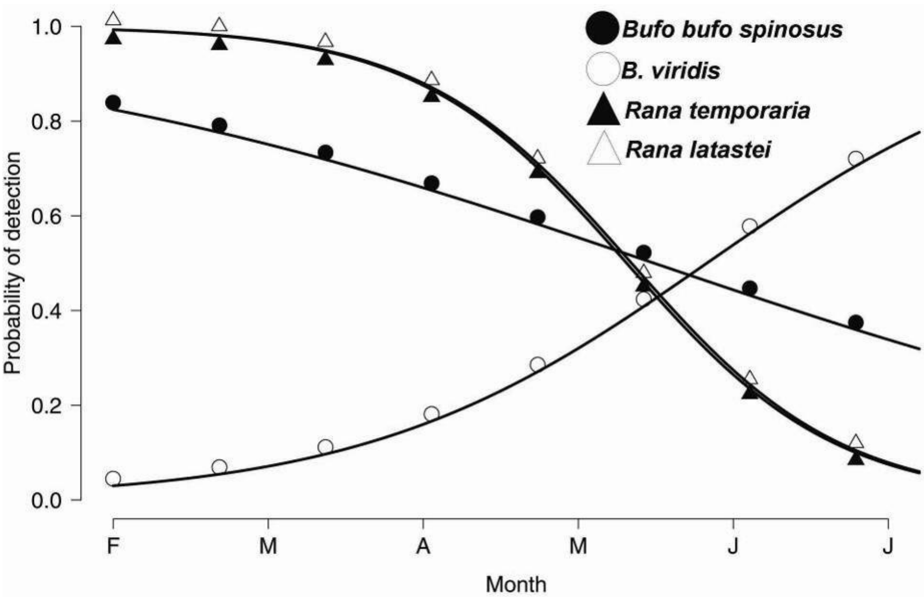
Model selection results for *R. latastei* ($\hat{c}$ = 9.34)

Model no.	Factors															K	ΔQAICc	Qweight	Qdeviance
Single factor groups																			
23		Ar		De		St										9	0.00	0.333	331.59
34		Ar	Ar^2	De	De^2	St										11	2.08	0.118	329.45
58											Fi	Pr	Pbb	Pbv	Pte	11	5.55	0.021	332.92
57											Fi					7	11.73	0.001	347.50
1																6	11.74	0.001	349.58
12	Ht															9	12.02	0.001	343.62
45							T		Ph	Ph^2						9	16.74	0.000	348.34
56							T	T^2	Ph	Ph^2						10	17.58	0.000	347.06
Sum																		0.474	
Multiple factor groups, linear																			
6		Ar		De		St					Fi					10	1.71	0.141	331.20
59	Ht	Ar		De		St										12	3.43	0.060	328.66
7		Ar		De		St					Fi	Pr	Pbb	Pbv	Pte	14	4.36	0.038	325.29
11	Ht	Ar		De		St					Fi					13	4.88	0.029	327.98
5		Ar		De		St	T		Ph	Ph^2						12	6.24	0.015	331.48
16		Ar		De		St	T		Ph	Ph^2	Fi					13	7.97	0.006	331.06
13	Ht	Ar		De		St					Fi	Pr	Pbb	Pbv	Pte	17	9.28	0.003	323.67
10	Ht	Ar		De		St	T		Ph	Ph^2						15	9.67	0.003	328.44
3	Ht										Fi					10	10.28	0.002	339.77
17		Ar		De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	17	10.35	0.002	324.74
4	Ht										Fi	Pr	Pbb	Pbv	Pte	14	10.65	0.002	331.59
9							T		Ph	Ph^2		Pr	Pbb	Pbv	Pte	14	10.72	0.002	331.66
18	Ht	Ar		De		St	T		Ph	Ph^2	Fi					16	11.14	0.001	327.72
19	Ht	Ar		De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	20	15.74	0.000	323.47
14	Ht						T		Ph	Ph^2	Fi					13	16.29	0.000	339.38
15	Ht						T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	17	16.58	0.000	330.97
8							T		Ph	Ph^2	Fi					10	16.73	0.000	346.22
2	Ht						T		Ph	Ph^2						12	17.81	0.000	343.04
Sum																		0.303	
Multiple factor groups, quadratic																			
27		Ar	Ar^2	De		St					Fi					11	3.42	0.060	330.78
28		Ar	Ar^2	De	De^2	St					Fi					12	3.94	0.046	329.18
20	Ht	Ar	Ar^2	De		St										13	5.16	0.025	328.26
21	Ht	Ar	Ar^2	De	De^2	St										14	5.44	0.022	326.38
29		Ar	Ar^2	De		St					Fi	Pr	Pbb	Pbv	Pte	15	6.45	0.013	325.22
37	Ht	Ar	Ar^2	De		St					Fi					14	6.78	0.011	327.72
38	Ht	Ar	Ar^2	De	De^2	St					Fi					15	7.03	0.010	325.80
30		Ar	Ar^2	De	De^2	St					Fi	Pr	Pbb	Pbv	Pte	16	7.70	0.007	324.29
24		Ar	Ar^2	De		St	T		Ph	Ph^2						13	7.80	0.007	330.90
25		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2						14	8.29	0.005	329.23
43		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi					14	9.67	0.003	330.61
26		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2						15	9.87	0.002	328.64
44		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi					15	10.16	0.002	328.93
39	Ht	Ar	Ar^2	De		St					Fi	Pr	Pbb	Pbv	Pte	18	11.43	0.001	323.62
33	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2						16	11.49	0.001	328.08
46		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi					16	11.65	0.001	328.23
35	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2						17	11.75	0.001	326.14
47		Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	18	12.48	0.001	324.66

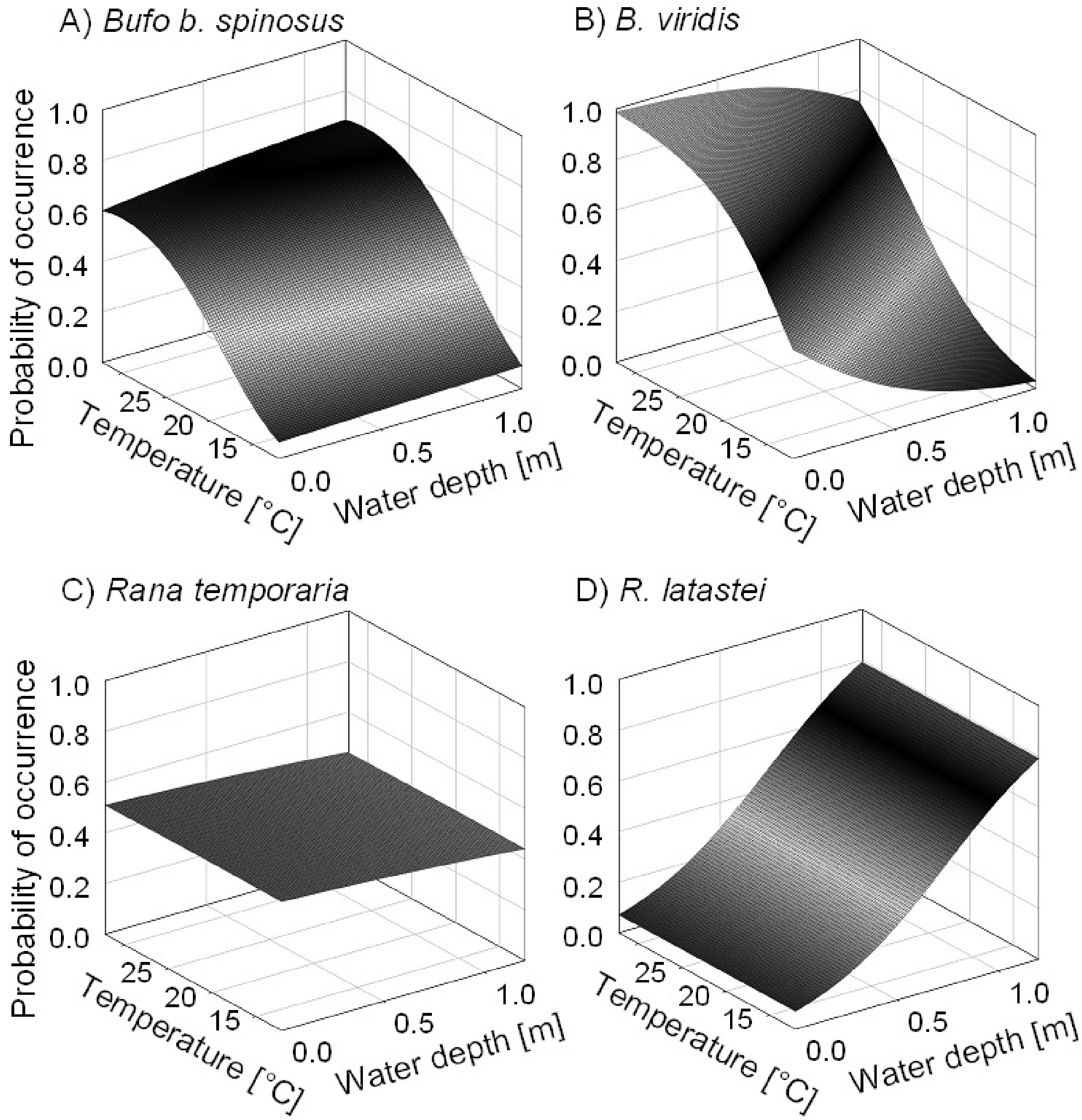
40	Ht	Ar	Ar^2	De	De^2	St					Fi	Pr	Pbb	Pbv	Pte	19	12.62	0.001	322.58
32							T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	15	12.88	0.001	331.64
50	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi					17	13.11	0.000	327.50
51	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi					18	13.30	0.000	325.49
36	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2						18	13.53	0.000	325.72
48		Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	19	13.65	0.000	323.61
52	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi					19	14.95	0.000	324.92
49		Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	20	15.70	0.000	323.43
31							T	T^2	Ph	Ph^2	Fi					11	17.73	0.000	345.10
41	Ht						T	T^2	Ph	Ph^2	Fi					14	17.73	0.000	338.67
53	Ht	Ar	Ar^2	De		St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	21	17.94	0.000	323.42
42	Ht						T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	18	18.77	0.000	330.96
22	Ht						T	T^2	Ph	Ph^2						13	19.05	0.000	342.14
54	Ht	Ar	Ar^2	De	De^2	St	T		Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	22	19.07	0.000	322.29
55	Ht	Ar	Ar^2	De	De^2	St	T	T^2	Ph	Ph^2	Fi	Pr	Pbb	Pbv	Pte	23	21.14	0.000	322.08
Sum																		0.222	
Total																		1.000	

Note: See Table 1 for abbreviations of factors. Model no. 1 = constant probability of occurrence (ψ). The top ranked model with ΔQAICc = 0 best approximates the data and models with ΔQAICc ≤ 2 are considered to receive substantial support from the data. Number of factors (K) and Akaike weights are given. When one model receives weights ≥ 0.9 there is no model selection uncertainty apparent. Factor year was included in every model to correct for its potential impact. Factor year was included in every model to correct for its potential impact.

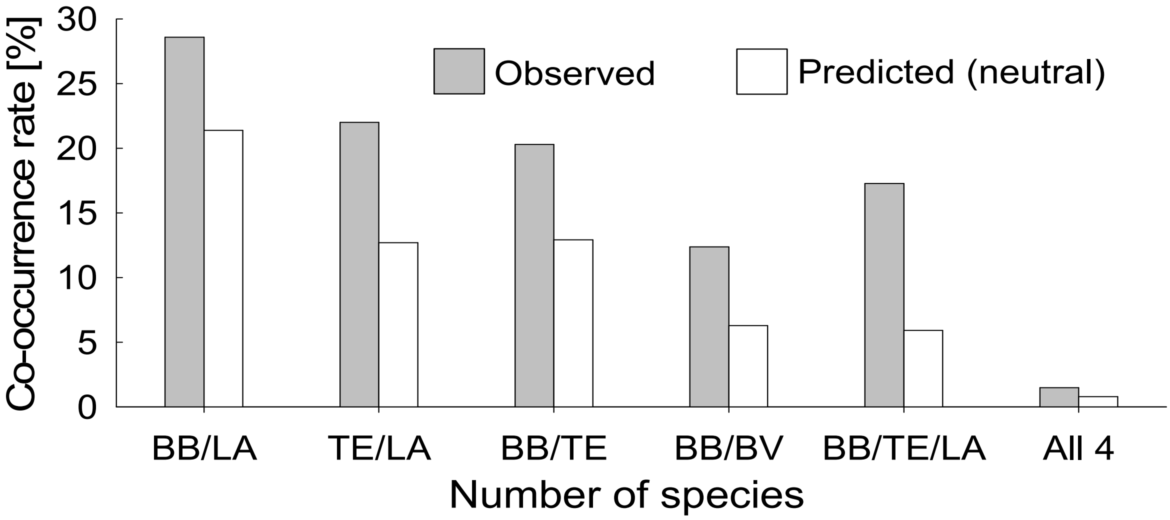
Appendix E. Predicted probability of detection (*p*) over the season, separated for the four species. All lines are thick, thereby denoting significant relationships (i.e. regression slopes did not include zero in confidence intervals).



Appendix F. Predicted probabilities of occurrence (ψ) in relation to the additive effects of temperature (T), water depth (De), and the quadratic effects of these factors, separately for (A) *Bufo b. spinosus*, (B) *B. viridis*, (C) *Rana temporaria*, and (D) *R. latastei*. We used 200 values of each factor within the range of observed factor values for the predictions. Factor values were z-standardized (mean = 0). The following model was used to predict probabilities of occurrence: $\mathrm{logit}(\psi) = \exp(\mathrm{Intercept}+\alpha T_i+\beta T_i^2+\gamma De_i+\delta De_i^2)/(\exp(\mathrm{Intercept}+1+\alpha Ti_i+\beta Ti_i^2+\gamma De_i+\delta De_i^2))$, where i are the different factor values and α, β, γ ,and δ are the regression slopes out of Table 4. The intercept was the regression slope of the habitat type "forest edge", which was used by all species.



Appendix G. Observed and predicted rates of co-occurrence. Co-occurrence rates are given for two, three, and four species. Predicted rates of co-occurrence (multiple species), assuming neutral processes, are the products of rates of occurrence of single species (see Results section). BB = *Bufo b. spinosus*, BV = *B. viridis*, TE = *Rana temporaria*, LA = *R. latastei*.



Appendix H. Factors used to predict the number of species in ponds (*n* = 353). Effect sizes (Beta), standard errors (SE), lower (LCI) and upper (UCI) 95% confidence intervals are given.

Code	Factors	Beta	SE	LCI	UCI
	Intercept	0.504	0.069	0.368	0.640
Ar	Area	0.364	0.100	0.168	0.561
Ar^2	$Area^2$	-0.052	0.018	-0.087	-0.016
De	Depth	0.384	0.081	0.225	0.544
De^2	$Depth^2$	-0.141	0.034	-0.208	-0.073
St	Structure for egg attachment	0.261	0.058	0.148	0.374
T	Temperature	0.332	0.056	0.222	0.442
T^2	$Temperature^2$	-0.170	0.049	-0.265	-0.075

Note: We used a general linear model (link function="Poisson") to predict species diversity (number of species) at the pond-level in relation to the additive and quadratic effects of abiotic factors ($Ar + Ar^2 + De + De^2 + St + T + T^2$). Factor values were z-standardized (mean = 0) prior to analysis. None of the factors included zero in confidence intervals. See Table 1 for description of factors. Habitat type was excluded as an explaining factor because species largely used habitat types similarly. The factors predation risk and the presence of fish were excluded as well. These factors covaried with the occurrence of anurans (see Fig. 1). Predation risk and the presence of fish do not increase the attractiveness of ponds for anurans, rather predators and fish prefer the same habitat characteristics as anuran species.

CHAPTER 5

Abiotic and biotic factors determine among-pond variation in anuran body size at metamorphosis in a dynamic floodplain: the pivotal role of river beds

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Abstract. Body size at metamorphosis is a critical trait in the life cycle of amphibians that affects population dynamics through survival and fecundity in later life. Despite the heavy use of amphibians as experimental model organisms, we poorly understand the mechanisms causing variation in metamorphic traits under natural conditions. Our main goal was to quantify the direct and interactive effects of abiotic and biotic factors on among-pond variation in body size at metamorphosis of anuran tadpoles (*Bufo b. spinosus*). The population was patchily distributed over the major habitats of a dynamic floodplain, the active tract and the riparian forest. The studied ponds differed with respect to hydroperiod, temperature, and predation risk. Warm ponds with more variable hydroperiod containing few predators were primarily located in the active tract, and ponds with opposite characteristics in the riparian forest.

Tadpoles from the active tract metamorphosed three weeks earlier and at a larger size than tadpoles from the riparian forest. In addition, population density at metamorphosis in the active tract was about one to two order of magnitudes larger than in the riparian forest. Larval mortality in the active tract was about 16% lower than in the riparian forest.

Spatial variation in body size at metamorphosis was goverend by direct and interactive effects of abiotic and biotic factors. Impacts of intraspecific competition on body size at metamorphosis were evident only at high temperature. Predation and intraspecific competition jointly reduced metamorphic size. At low intraspecific competition, predation limited growth while at high competition, predation increased growth.

The ponds in the active tract seem to be pivotal for the performance of anuran larvae and hence population persistence. The maintenance of this habitat type depends on a natural river bed and flow regime. River restorations seem therefore promising to increase the availability of high quality habitats that improve larval performance.

Introduction

Size and growth rate are fundamental traits that control the performance of plants and animals (Alford, 1999; Stearns, 1992). These traits vary in time and space (Slatkin, 1974; Wauters, Vermeulen, Van Dongen et al., 2007), thereby affecting the abundance and distribution of species (Gutierrez & Menendez, 1997; Loehle, 2006). For species with complex life cycles, body size at metamorphosis is a critical trait influencing survival and fitness in later life (Smith, 1987). Despite the importance of body size for population dynamics, the factors that govern spatial variation in life history traits are not yet sufficiently explored.

Metamorphosis is a life history transition, which is usually associated with a change of habitat and behavior (Wilbur, 1980). Metamorphosis occurs in taxa such as molluscs, insects, and amphibians (Werner, 1988). Individuals that are larger at metamorphosis are expected to perform better later in life than smaller individuals (Altwegg & Reyer, 2003; Berven, 1990; Smith, 1987). Furthermore, population models showed that equilibrium densities or population growth rates can be highly sensitive to variation in juvenile survival (Biek, Funk, Maxell *et al.*, 2002; Lampo & De Leo, 1998). Therefore, body size early in the life cycle is fitness relevant, and can be important for local population dynamics. Identifying the key factors impacting body size at metamorphosis therefore improves our understanding of population dynamics of species with complex life cycles and may help to develop conservation strategies. In this context, amphibians are of particular interest, given their global population decline (Houlahan, Findlay, Schmidt *et al.*, 2000).

The impact of abiotic and biotic factors on body size variation of anuran larvae has been well explored in mesocosm experiments. These experiments helped to elucidate the factors and mechanisms that regulate metamorphic size (Alford, 1999). However, it is unclear to what extent experimental treatments reflect natural conditions, and there is concern that mesocosm studies may overestimate effect sizes (Skelly & Kiesecker, 2001; Werner, 1998). Under natural conditions, abiotic and biotic factors interact and change dynamically in time and space (Dunson & Travis, 1991). However, few studies analyzed spatial variation in life history traits at metamorphosis under natural conditions (Gray & Smith, 2005; Petranka, 1984; Reading, 2003; Reading & Clarke, 1999). Such studies are in need to justify experimentally measured effect sizes and to evaluate their relevance for natural population dynamics (Werner, 1998).

We studied among-pond variation in body size at metamorphosis of larvae of the common toad (*Bufo bufo spinosus*) under natural conditions. The common toad is a dominant species in temporary and permanent ponds of dynamic braided floodplains (Kuhn, 2001; Tockner, Klaus, Baumgartner *et al.*, 2006). Braided floodplains are composed of two major habitats, the active tract that is frequently reworked by floods and the riparian forest that fringes the active tract. Ponds in the active tract are more variable in hydroperiod and sun-exposed, while ponds in the riparian forest are more permanent, shaded, and morphologically stable. This results in predictable differences in hydroperiod, temperature, and predation risk. Ponds of the active tract are in general warmer and more productive, and contain less predators than ponds in the riparian forest (Wellborn, Skelly & Werner, 1996). The expectation is that the more variable hydroperiod and higher temperatures of ponds in the active tract select for short larval periods and consequently small-sized metamorphs. In cool and more permanent ponds of the riparian forest, tadpoles are expected to metamorphose later in the season and at large body size (Berrigan & Charnov, 1994). However, different predation risks in these major habitats may have antagonistic effects, i.e. low predation risk in the active tract may select for long larval periods and large size at metamorphosis while high predation risk in the riparian forest may select for the opposite (Skelly & Werner, 1990; Travis, Keen & Juilianna, 1985). These opposing selection pressures might result in similar body size at and time to metamorphosis in these major habitats.

We quantified body size at metamorphosis of a patchily distributed population of *B. b. spinosus* tadpoles in ponds of the active tract and of the riparian forest in an unconstrained alpine floodplain. Our main goals were i) to determine whether tadpole performance (body size at metamorphosis, growth rates) and population density at metamorphosis in the two main habitat types is different, and ii) to quantify the impact of factors governing differences in larval performance between habitat types and among ponds in general. For the second question, our focus was on among-pond variation in body size at metamorphosis, an important life history trait for species with complex life cycles.

Methods

Study site

The study was conducted from 14 March 2006 until 2 July 2006 in an island-braided floodplain along the 7th order Tagliamento River in northeastern Italy (46°N, 12°30'E) (Fig. 1a). The Tagliamento (catchment area: 2580 km^2) originates at 1000 m asl in the southern fringe of the European Alps and flows almost unimpeded by dams for 172 km to the Adriatic Sea. Unlike most European rivers, the river retains its essentially pristine morphological and hydrological characteristics (Ward, Tockner, Edwards *et al.*, 1999).

The study site (river-km 79.8 -80.8; 135 m asl) covered a 800-m wide active tract (1.6 km^2) and the adjacent riparian forest (right bank). The active tract comprised a spatiotemporally complex mosaic of vegetated islands, a braided network of main and secondary channels, backwaters and ponds, embedded within a matrix of exposed gravel sediments (Petts, Gurnell, Gerrard *et al.*, 2000) (Fig. 1). Within the riparian forest ponds are distributed along an alluvial channel.

The habitat mosaic within the study area is frequently reworked by floods (Arscott, Tockner, van der Nat *et al.*, 2002). This river section was chosen because both habitat heterogeneity (Arscott, Tockner, van der Nat *et al.*, 2002) and amphibian diversity are high (Tockner *et al.*, 2006). The study species is abundant both within the active tract and the riparian forest.

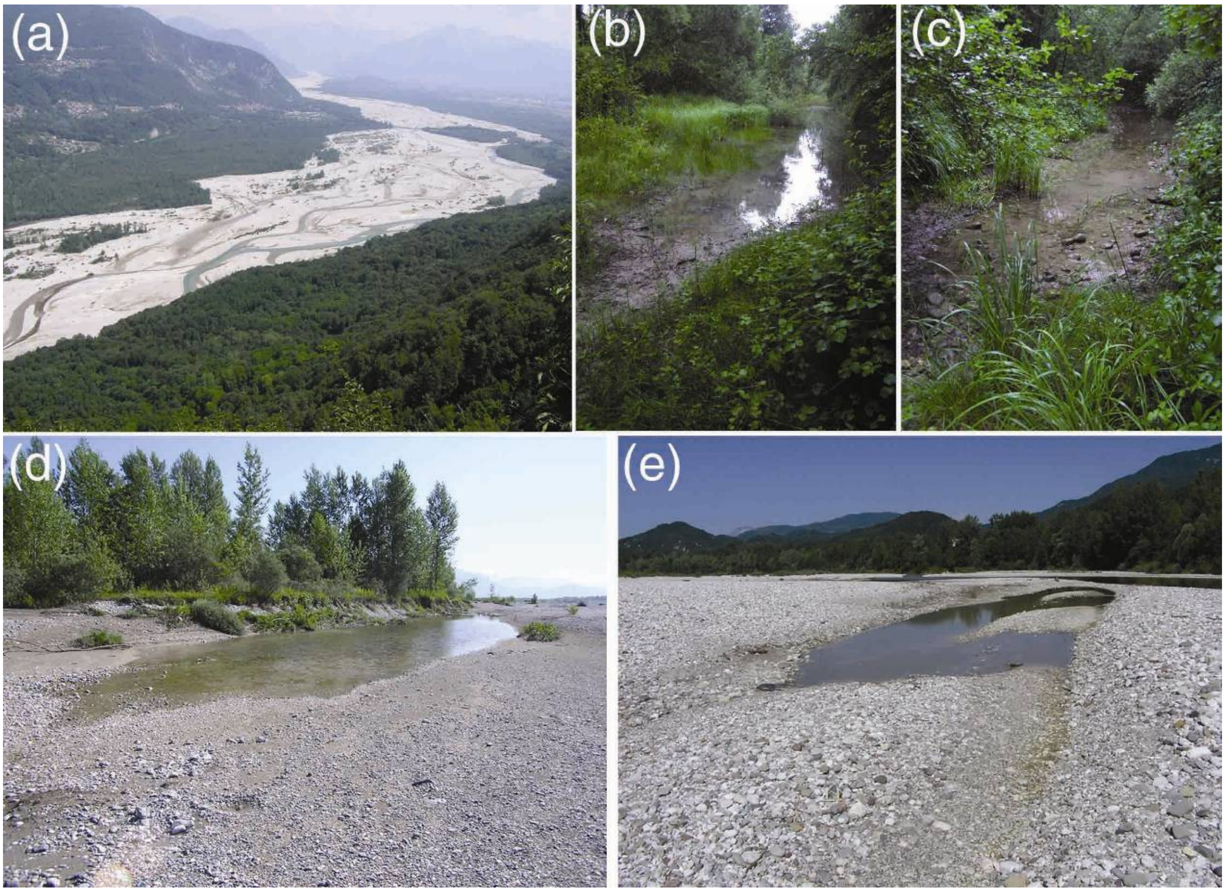

Figure 1. Oblique photo of the (a) study site taken from Monte Ragogna (L. Indermaur, 2006). (b,c) two characteristic ponds located within the riparian forest, and (d,e) within the active tract.

Study species

Bufo b. spinosus (European common toad) was selected to study spatial variation in tadpole size at metamorphosis. *B. b. spinosus* is widespread in Mediterranean countries, known as an early breeder with a fixed breeding time and a preference for large permanent waters (Giacoma & Castellano, 2006). This species, however, shows considerable behavioral plasticity when breeding in unpredictable environments (Kuhn, 2001).

Eleven amphibian species were present in the study section (Tockner *et al.*, 2006). The four most frequent species were *B. b. spinosus*, *B. viridis*, *R. temporaria*, and *R. latastei*. The larvae of *B. b. spinosous*, the predominant species, co-occurred with the dominant Italian Agile frog (*Rana latastei*) and the European common frog (*R. temporaria*). Common toads co-occurred with Agile frogs (*R. dalmatina*) only within the riparian forest. Green toads (*B. viridis*) only co-occurred with common toads within the active tract.

Data collection

Pond selection. All ponds (pond surface area ≥ 1 m^2, water water depth > 0.05 m) in the active tract (n = 92) and in the riparian forest (n = 49) of the study area were mapped four times from February to July 2006. *B. b. spinosus* laid eggs in about half of the ponds of both the active tract and the riparian forest. From all ponds, we randomly selected 25 ponds in the active tract and 12 ponds in the riparian forest for measuring body size and explanatory factors (Table 1). Egg laying within the selected ponds was completed within a week. Hence, tadpoles within the same pond can be regarded as single age-cohort.

Pond attributes. We measured 14 abiotic and biotic factors that were expected to affect body size of tadpoles (Alford, 1999) (Table 1). These factors included competition (intraspecific and interspecific), predation (an index describing predation risk excluding fish, fish presence), pond morphology (mean pond surface area, mean water depth), pond condition (specific conductance, oxygen concentration, maximum temperature, pH, algae cover, hydroperiod length as the number of days ponds contained), and tadpole age at metamorphosis which is equal to the duration of the larval period (number of days from egg laying until metamorphosis). Details on sampling intervals and measuring methods are presented in Table 1. The factors “pH”, and “water depth” were omitted for analyses because they were highly correlated with “oxygen concentration” and “hydroperiod length”, respectively (Appendices A,B). Spatial variation in abiotic and biotic factors were explored using a larger data set (*n* ponds = 353) that was collected in 2005 and 2006 (Fig. 2).

Table 1. Factors used for predicting variation in log-body size at metamorphosis. Factors in brackets were correlated with other factors (see Appendix A) and hence not used for analyses. Ci and Ct were estimated for every sampling interval (weekly). For other factors we used mean values in the analyses as they were not measured in weekly intervals or did not overlap temporally with tadpole sampling.

Code	Factor	Sampling interval	Measuring details	Reference[a]
Age	Number of days from egg laying until sampling	Weekly	Weekly egg clutch surveys of all ponds	Berven, 1990
Al	Algae availability [%]	Monthly (4 times)	Visual quantification of algae cover	Mallory & Richardson, 2005; Peterson & Boulton, 1999
Ar	Mean pond surface area [m^2]	Monthly (4 times)	dGPS (Trimble GeoXT, Zurich)	Laurila, 2000
Ca	Intraspecific competition [number of larvae *B. b. spinosus*/m^2]	Weekly	Sweep netting and funnel traps proportional to water area	Griffiths, 1991; Morin, 1983
Ci	Interspecific competition [number of larvae other than *B. b. spinosus*/m^2]	Weekly	Sweep netting and funnel traps proportional to pond surface area	Teplitsky & Laurila, 2007
Cy	Specific conductance [µS/cm]	Monthly (4 times)	WTW LF 340[b]	McKibbin, Dushenko, Vanaggeler *et al.*, 2008
(De)	Water depth [m]	Weekly	Maximum water depth	Pearman, 1993
Fi	Fishes ≥ 10 cm (present/absent)	Monthly (4 times)	Visually	Watt, Nottingham & Young, 1997
Hp	Hydroperiod length (number of days ponds contained water)	Weekly		Wellborn, Skelly & Werner, 1996; Wilbur & Collins, 1973
Ox	Oxygen concentration [mg/l]	Monthly (4 times)	WTW Oxi 340[b]	Wassersug & Seibert, 1975
(Ph)	pH [H^+]	Monthly (4 times)	WTW pH 340[b]	Beebee, 1986; Cummins, 1986
Pr	Predation (index: 0-1)	Once	Sweep netting and funnel traps proportional to pond surface area[c]	Herreid & Kinney, 1966; Skelly & Werner, 1990
Si	Site (two levels: active tract, forest)		Once classified	Skelly, Freidenburg & Kiesecker, 2002

Sm	Mean log-body size per pond and occasion [pixel/mm^2] (response variable)	Weekly	ImageJ V 1.4.0, National Institute of Health, Maryland, USA	
T	Mean maximum water temperature [°C]	Hourly	Thermochron ibutton loggers DS1921G	Herreid & Kinney, 1967

[a] Studies that found evidence that specific factors affect life history traits of tadpoles

[b] Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany

[c] Sum of individuals of newts (*Triturus carnifex, T. vulgaris*), snakes (*Natrix natrix*), insects (larvae and adults of *Dytiscus marginalis, Aeshna sp.)**number of predator groups present (newts, snakes, insects), normalized between 0 and 1. The weighting factor "number of predator groups" was included as the interactive effects of various predator taxa are considered more dangerous than of single taxa.

Tadpole sampling. Tadpoles were sampled at regular intervals to quantify population density/competition and body size from which we derived growth rates. Tadpoles were caught on two consecutive days at weekly intervals. Sampling was done over a period of 4 to 14 weeks, depending on the duration of the larval period. We used funnel traps to catch tadpoles (Fig. 2b). Traps were exposed at least 0.5 hours when trapping success was high and up to 4 hours when trapping success was low. Traps were randomly distributed and the number of traps per pond (range: 1-14) was in proportion to the water area. Dip-netting was used in addition to funnel traps when less than 10 tadpoles of *B. b. spinosus* were caught in the traps. Sampling started when larvae were swimming (Gosner developmental stage 26) (Gosner, 1960), which was on average 26 days after egg laying in the active tract and 31 days after egg laying in the riparian forest. Sampling ended shortly before metamorphosis (Gosner developmental stage 41). In two ponds in the active tract and one pond in the riparian forest all tadpoles died before metamorphosis. These ponds were included for analyses as developmental stage 41 was almost reached.

We used tadpole population density of *B. b. spinosus* as an index for intraspecific competition and tadpole population density of all other species to quantify interspecific competition. We estimated tadpole population density using capture-mark-recapture methods. At first capture occasions within a week, all tadpoles caught were batch-marked with a temporary visible neutral red dye staining solution (Viertel, 1980) (Fig. 2c). Marked tadpoles were released immediately after marking at various locations of their ponds. The following day tadpoles were caught again at the same ponds. Unmarked and marked tadpoles were counted and tadpoles released afterwards (Fig. 2a).

Population density. We estimated population size per m^2 using Baileys' formula (Bailey, 1952): (n animals caught and marked at first capture occasion + 1)*(n animals caught at second capture occasion + 1))/(n animals caught at first and second capture occasion + 1)). This estimate was then divided by pond surface area. The use of Baileys' formula requires that the population is closed, i.e., population size is not influenced by mortality and emigration as well that tags are neither lost nor overlooked. We minimized mortality-related bias in population size by separating marking and recapture occasions by one day only. Bias due to emigration was unlikely, as we stopped sampling when the proportion of tadpoles with forelegs was at most 10%. Tags were clearly visible up to 3 days after tagging but disappeared within less than one week. By sampling at weekly intervals we avoided double-counting of tadpoles that were tagged the previous week. Hence, all underlying assumptions of the method were met as closely as possible. In line with others (Sinsch, 1997; Viertel, 1980), we did not find any impact of marking method on mortality and behavior.

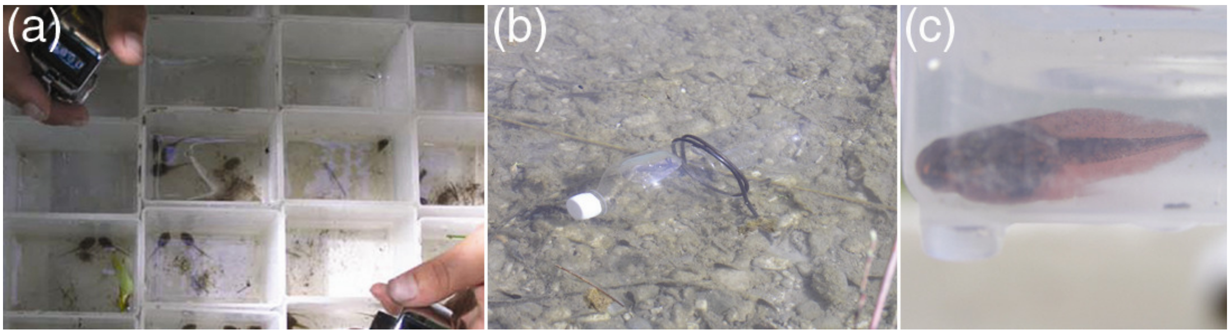

Figure 2. (a) The number of tadpoles were counted separately per species. Tadpoles were subdivided in boxes to facilitate counting and identification of marked larvae; (b) Funnel trap used to catcth tadpoles, attached with a wire to exposed gravel sediments; (c) Larvae of *Rana temporaria*, marked with neutral red dye.

Body size. Body size of *B. b. spinosus* larvae was quantified by processing digital photographs that were taken at weekly intervals. We randomly selected and photographed between 12 and 35 tadpoles per pond and occasion within a flat basin (50x40 cm). A milimeter scale was attached to the bottom to correct for spatial scale. Photographs were processed using software ImageJ V 1.4.0 (Abramoff, Magelhaes & Ram, 2004), which automatically counts the number of tadpoles as well as the size of each tadpole (number of pixels). In total, body size of 4117 individual tadpoles was measured. From these individual measures we derived mean body size per pond and occasion, which we used for the analyses (*n* means across all ponds and occasions = 209).

Statistical analysis

Growth rate. We calculated the growth rate as a daily proportion of body size, solving the following equation for "rate" as suggested elsewhere (Anholt, Werner, & Skelly, 2000): body size at metamorphosis = body size at first sampling * $(1 + \text{rate})^{\text{age}}$. Differences in growth rate between tadpoles from the active tract and the riparian forest were analysed using ANCOVA, taking "log-body size at first sampling" as a covariate and "site" as a fixed factor. Growth rates were ln-transformed to assure normally distributed residuals.

Modelling among-pond variation in body size at metamorphosis. We used an information-theoretic approach (Burnham & Anderson, 2002) to find the model that best explains among-pond variation in body size at metamorphosis. We fitted 38 candidate models to the data. Each model reflects a hypothesis and the factors used are based on previous studies (Tables 1 and 2). We grouped explaining factors into competition, predation, pond morphology, and pond condition. We asked whether variation in body size at metamorphosis is determined by a single group of factors or by the combinations of different groups of factors and by interactions between factors. For example, model no. 18

hypothesizes that the effects of water area and predation risk are independent while model no. 19 hypothesizes that the effects of water area interact with predation risk. To reduce the number of explanatory factors, we either used intraspecific or interspecific competition in the models, but not both intra- and interspecific competition in the same model. The factors "site" (two levels: active tract, riparian forest) and "age" were included as additive effects in every model.

Table 2. Models used for predicting variation in tadpole log-body size at metamorphosis. The factors "Age" (as mean at metamorphosis=80 days), "Si" (Site: active tract, forest) were included in every model. Models with interactions are in italics and models with intraspecific competition are in bold. See Table 1 for abbreviations of factors.

Model no	Factors	Explanation
1	**Ca**	Intraspecific competition
2	Ci	Interspecific competition
3	**Ca+Ox**	Intraspecific competition and condition
4	**Ca+Ox+Ca*Ox**	*Intraspecific competition and condition*
5	Ci+Ox	Interspecific competition and condition
6	Ci+Ox+Ci*Ox	*Interspecific competition and condition*
7	**Ca+Ox+T**	Intraspecific competition and condition
8	**Ca+Ox+T+Ca*Ox**	*Intraspecific competition and condition*
9	**Ca+Ox+T+Ca*Ox+Ca*T**	*Intraspecific competition and condition*
10	Ci+Ox+T	Interspecific competition and condition
11	Ci+Ox+T+Ci*Ox	*Interspecific competition and condition*
12	Ci+Ox+T+Ci*Ox+Ci*T	*Interspecific competition and condition*
13	**Ca+Al**	Intraspecific competition and condition
14	**Ca+Al+Ca*Al**	*Intraspecific competition and condition*
15	Cy+Ox+T	Condition
16	Cy+Ox+T+Ox*T	*Condition*
17	Pr+Ar+Fi	Morphology and predation
18	Pr+Ar	Morphology and predation
19	Pr+Ar+Pr*Ar	*Morphology and predation*
20	Ar+Hp	Morphology
21	**Ca+Ar+Ox+T+Cy+Pr**	Intraspecific competition, morphology, condition, predation
22	**Ca+Ar+Hp+Ox+T+Cy+Pr**	Intraspecific competition, morphology, condition, predation
23	**Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox**	*Intraspecific competition, morphology, condition, predation*
24	**Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox+Ca*T**	*Intraspecific competition, morphology, condition, predation*
25	**Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox+Ca*T+Pr*Ar**	*Intraspecific competition, morphology, condition, predation*
26	**Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox+Ca*T+Ca*Pr**	*Intraspecific competition, morphology, condition, predation*
27	**Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*T+Ca*Pr**	*Intraspecific competition, morphology, condition, predation*
28	**Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox+Ca*Pr**	*Intraspecific competition, morphology, condition, predation*
29	Ci+Ar+Ox+T+Cy+Pr	Interspecific competition, morphology, condition,

		predation
30	Ci+Ar+Hp+Ox+T+Cy+Pr	Interspecific competition, morphology, condition, predation
31	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox	*Interspecific competition, morphology, condition, predation*
32	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox+Ci*T	*Interspecific competition, morphology, condition, predation*
33	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox+Ci*T+Pr*Ar	*Interspecific competition, morphology, condition, predation*
34	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox+Ci*T+Ci*Pr	*Interspecific competition, morphology, condition, predation*
35	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*T+Ci*Pr	*Interspecific competition, morphology, condition, predation*
36	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox+Ci*Pr	*Interspecific competition, morphology, condition, predation*
37	**Ca+Ar+Hp+Ox+T+Cy+Al+Pr+Fi+Ca*Ox+Ca*T+ Ca*Pr+Ca*Al+Ox*T+Pr*Ar**	*All factors and interactions*
38	Ci+Ar+Hp+Ox+T+Cy+Al+Pr+Fi+Ci*Ox+Ci*T+ Ci*Pr+Ci*Al+Ox*T+Pr*Ar	*All factors and interactions*

We fitted linear mixed effects models (package lme4, random=~ 1|pond/occasion, method=”ML”) in R (V 2.4.0) (R Development Core Team 2007) to the data. The repeated body-size measures over time (occasion) were specified as nested random effects per pond in the model. All continuous explanatory factors were z-standardized prior to analysis. Body size was log-transformed to assure normally distributed residuals.

Predicting variation in body size at metamorphosis. To explore and show graphically the direct and interactive effects of factors on variation in log-body size at metamorphosis, we applied predictions using the best selected model. For example, to show the interactive effects of intraspecific competition and temperature, we predicted variation in log-body size for every combination of 161 competition values (observed range: 0 to 8000 tadpoles/m^2) and 11 temperature values (observed range: 17-27°C). For the factors specific conductance and hydroperiod length we used 100 values within the range of observed factor values. Other factors in the model were held constant using mean values (i.e., zero for standardized explanatory factors). We used 80 days for the factor “age”, which corresponds to occasion 8 and the point where body size was largest on average. Factor “site” was multiplied by 1, which corresponds to the riparian forest. Mean-predictions and confidence intervals were obtained by bootstrapping (1000 iterations).

Results

Environmental gradients

Predation risk increased with the length of the hydroperiod (Appendices A and B, Fig. 3a). Low predation risk mostly occurred in the ponds of the active tract. Temperature was higher in ponds of the active tract than in ponds of the riparian forest (Fig. 3b). Ponds with hydroperiods less than 40 days were absent in the riparian forest (Figs 3c and 3d). Ponds > 500 m^2 were absent in the riparian forest (Figs 3e and 3f). In summary, predation risk, temperature, pond surface area, water depth, and specific conductance (s. below) constituted the major environmental gradients.

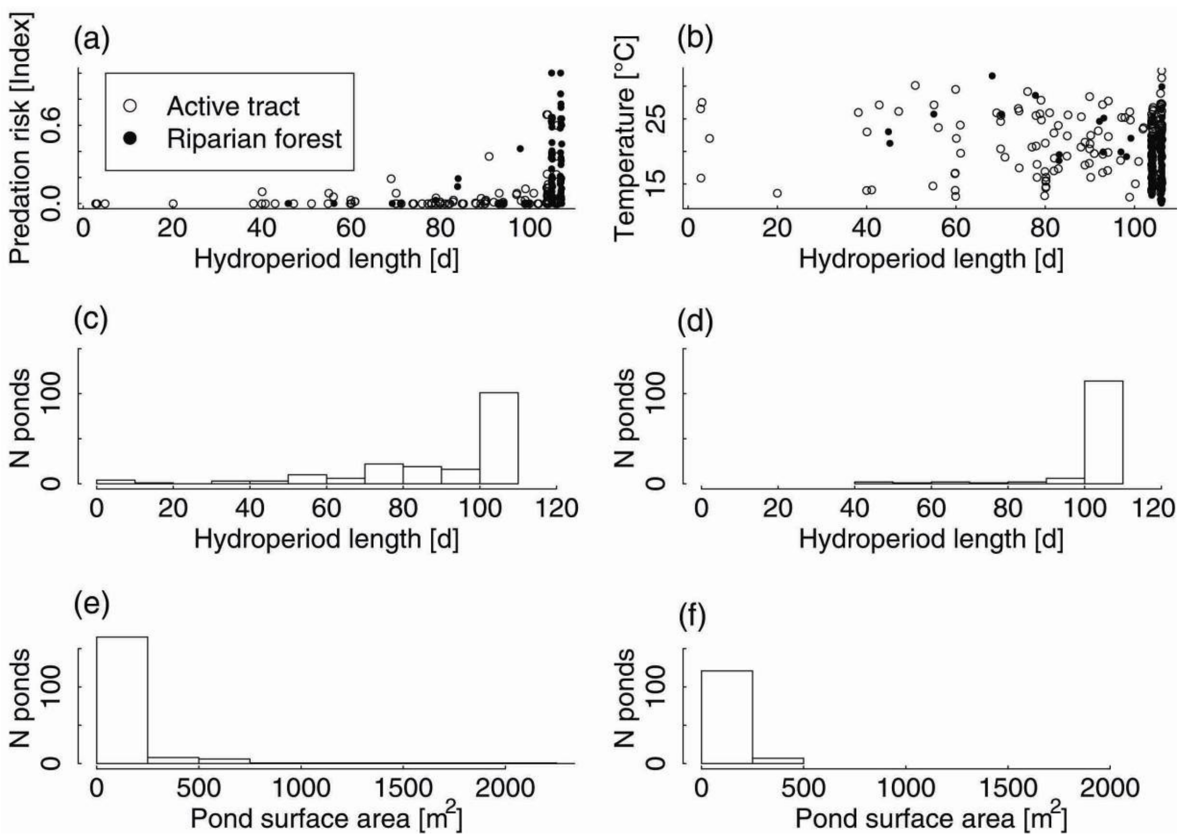

Figure 3. Relationships between (a) predation and (b) temperature with hydroperiod length as well as the distribution of ponds (c,d) across gradients in hydroperiod, and (e,f) pond surface area, separately for the active tract and the riparian forest. These graphs are based on data of 2005 and 2006, with a total number of 353 ponds.

Differences in larval performance between the active tract and the riparian forest

Characterization of study ponds. Specific conductance was on average 14% higher in the active tract than in the riparian forest (Table 3). Ponds in the active tract had higher oxygen concentration, were warmer, larger and shallower than ponds in the riparian forest (Table 3). Furthermore, hydroperiod length, which was positively related to water depth, was more variable and on average one week shorter in the active tract than in the riparian forest (Table 3, Fig. 3). Predation risk was on average about six times lower in the active tract than in the riparian forest, while intraspecific competition was similar in the two major habitats.

Table 3: Descriptive statistics for life history traits and abiotic and biotic factors for the active tract and the riparian forest. Factors in brackets were not used for modelling as they were highly correlated with other factors (see Appendix B). Sh=log-body size at first sampling. All factors, except Age, Sh, and Sm are mean values over the entire study period. See Table 1 for abbreviations of other factors.

		Site							
		Active tract				Riparian forest			
Code	Factor	Mean	SD	Range		Mean	SD	Range	
Age	Age at metamorphosis	56.71	17.73	35	93	82.68	12.45	62	100
Al	Algae cover	24.5	10.5	0	91.25	22.25	8.75	0	82.5
Ar	Pond surface area	65.66	120.24	0.99	506.41	55.46	47.08	21.95	189.02
Ca	Intraspecific competition	731.20	1588.48	0.00	7137.09	549.24	1427.82	0.00	8274.86
Ci	Interspecific competition	37.27	98.91	0.00	625.76	106.01	313.95	0.00	2364.12
Cy	Specific conductance	546.16	108.09	152.25	652.62	470.36	113.94	291.25	598.83

(De)	Water depth	0.28	0.15	0.09	0.69	0.39	0.24	0.20	1.00
Hp	Hydroperiod length	97.23	12.92	56.00	104.00	104.00	0.00	104.00	104.00
Ox	Oxygen	8.82	2.52	3.95	20.80	8.39	2.87	5.18	14.45
(Ph)	pH	7.83	0.24	7.57	8.86	7.80	0.28	7.50	8.32
Pr	Predation	0.09	0.09	0.00	0.34	0.51	0.32	0.12	1.00
(Sh)	Log-body size at first sampling	4.87	0.37	3.91	5.90	4.69	0.26	4.20	5.15
Sm	Log(body size at metamorphosis)	5.27	0.42	3.91	6.18	5.10	0.26	4.20	5.72
T	Temperature	23.55	2.53	17.43	26.75	21.09	1.59	17.88	23.43

Body size. Tadpoles within ponds of the active tract had on average a larger body size than tadpoles from ponds of the riparian forest, both at first sampling, and at metamorphosis (Table 3, Fig. 4a). Owing to the large variation, these differences, were however not significant when quantifying the separate and combined effects of the factors site (active tract, riparian forest) and age on log(body size at first sampling) (GLM: site: $t = 0.589$, $P = 0.560$; age: $t = 0.332$, $P = 0.742$; site*age: $t = 0.444$, $P = 0.660$). Similarly, the separate and combined effects of site, age, and log(body size at first sampling) had no significant effects on log(body size at metamorphosis) (site: $t = 1.001$, $P = 0.325$; age: $t = 0.086$, $P = 0.932$; log(body size at first sampling): $t = 1.500$, $P = 0.144$; site*log(body size at first sampling): $t = 1.036$, $P = 0.308$; age*log(body size at first sampling): $t = 0.070$, $P = 0.944$, site*age: $t = 0.878$, $P = 0.387$, site*age*log(body size at first sampling): $t = 0.889$, $P = 0.381$).

Growth rate. Tadpoles from the active tract grew significantly faster (mean ± SD in % pixels/d: 0.94 ± 0.49) than tadpoles from the riparian forest (mean ± SD in % pixels/d: 0.57 ± 0.21) (ANCOVA: "log(body size at first sampling)": $F_{1,34} = 7.461$, $P = 0.010$; fixed factor "site": $F_{1,34} = 7.697$, $P = 0.009$) (Fig. 4b). In addition, the larval period of tadpoles (age at metamorphosis) from the active tract was on average 26 days shorter than of tadpoles from the riparian forest (Table 3) ($t = 5.06$, $P < 0.001$).

Population density. Average population density at first sampling was similar in ponds of the active tract and the riparian forest (mean ± SD per m^2, range: active tract: 1256.1 ± 2125.9, 2.3-7137.1; riparian forest: 1610.1 ± 2458.4, 130.6-8274.8) (t = 1.476, P = 0.149) (Fig. 4c). However, population density at metamorphosis of ponds in the active tract was considerably larger than in ponds of the riparian forest (mean ± SD per m^2, range: active tract: 489.1 ± 1286.2, 0-4855.4; riparian forest: 12.1 ± 19.6, 0-59.9) (t = 2.767, P = 0.010) (Fig. 4d). The percentage of hatchlings that died until metamorphosis was on average 16% lower in the active tract than in the riparian forest (mean ± SD in %: range: active tract: 82.3 ± 22.4, 28.8-100; riparian forest: 98.9 ± 1.8, 94.2-100).

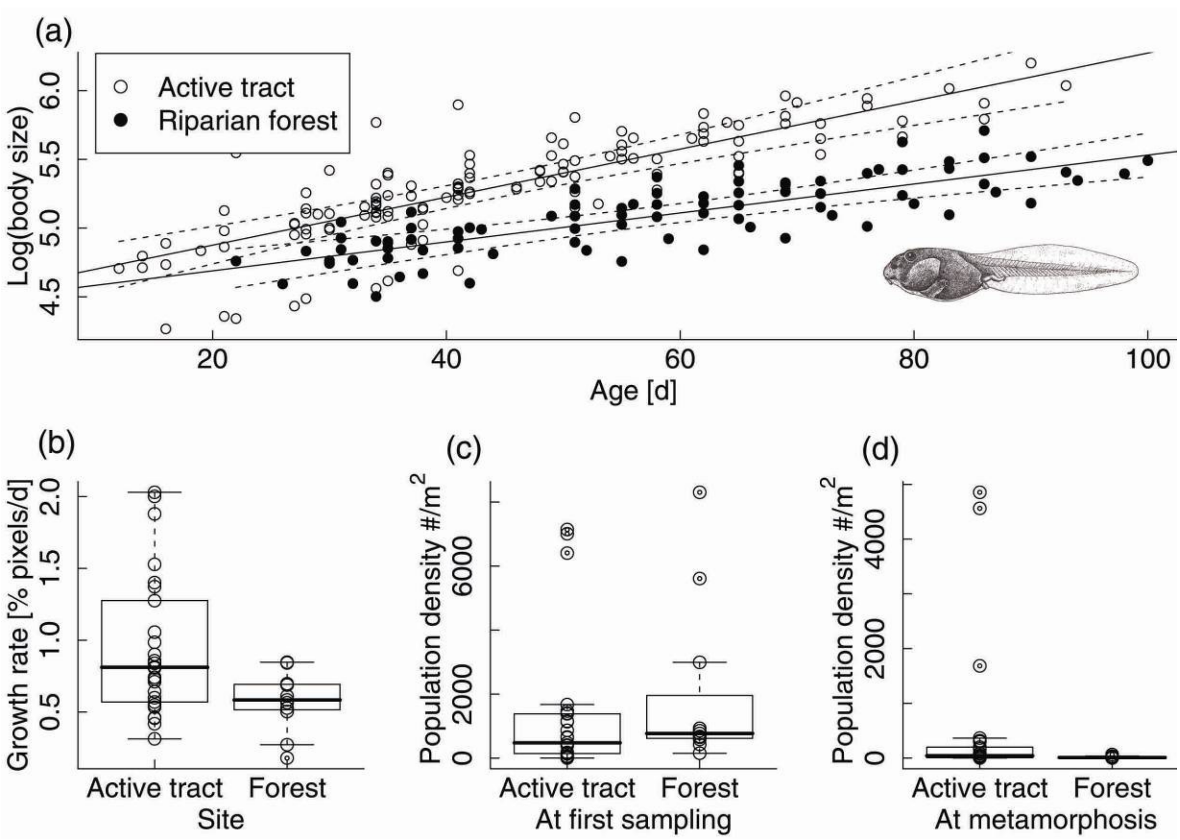

Figure 4. (a) Predicted log-body size in relation to age, separately for the active tract and the riparian forest. Differences in (b) growth rates (pixels/day), (c) population density at first sampling, and (d) at metamorphosis between the active tract and the riparian forest. Dashed lines are 95% confidence intervals.

Direct and interactive effects of abiotic and biotic factors on body size at metamorphosis

Model ranking. The top-ranked model (Table 4, no. 26, Akaike weight = 50.7%) included the effects of specific conductance, temperature, oxygen, pond surface area, hydroperiod length, age, site, intraspecific competition, and predation as well as the interactions intraspecific competition*predation risk, intraspecific competition*temperature, and intraspecific competition*oxygen concentration. The second-ranked model differed from the top-ranked model only the interaction intraspecific competition*oxygen concentration. This interaction did not improve model fit substantially (see likelihood, Table 4, no. 27). All other models were poorly supported by the data (Table 4).

Table 4. Model selection results for predicting variation in log-body size at metamorphosis of *B. b. spinosus*-tadpoles, sorted after Akaike's small sample information criterion scores (ΔAICc). The factors "age" (as mean at metamorphosis=80 days) and "site" were included in every model to correct for their potential effects on log-body size. The top ranked model with ΔAICc = 0 best approximates the data and models with ΔAICc ≤ 2 are considered to receive substantial support from the data. Number of estimated parameters (*K*), log-likelihood (*LL*), model weights (ωi) and evidence ratios (ER) are given. ER are the ratio of model weight of a particular model in relation to the top ranked model. When one model receives ωi ≥ 0.9, there is no model selection uncertainty apparent. See Table 1 for abbreviations of factors.

Model no.	Factors	*K*	*LL*	ΔAICc	Weights	ER
26	Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox+Ca*T+Ca*Pr	16	31.9	0.0	0.507	1.0
27	Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*T+Ca*Pr	15	30.7	0.1	0.489	1.0
37	Ca+Ar+Hp+Ox+T+Cy+Al+Pr+Fi+Ca*Ox+Ca*T+ Ca*Pr+Ca*Al+Ox*T+Pr*Ar	21	33.1	9.7	0.004	131
24	Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox+Ca*T	15	22.5	16.6	0.000	3.99E+03
25	Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox+Ca*T+Pr*Ar	16	22.5	18.9	0.000	1.29E+04
28	Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox+Ca*Pr	15	20.6	20.4	0.000	2.74E+04
9	Ca+Ox+T+Ca*Ox+Ca*T	11	8.37	35.7	0.000	5.54E+07
23	Ca+Ar+Hp+Ox+T+Cy+Pr+Ca*Ox	14	11.1	37.0	0.000	1.11E+08
14	Ca+Al+Ca*Al	9	5.25	37.5	0.000	1.37E+08
8	Ca+Ox+T+Ca*Ox	10	2.33	45.5	0.000	7.63E+09
4	Ca+Ox+Ca*Ox	9	1.19	45.6	0.000	7.91E+09
35	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*T+Ci*Pr	15	7.42	46.7	0.000	1.39E+10

32	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox+Ci*T	15	7.36	46.8	0.000	1.47E+10
30	Ci+Ar+Hp+Ox+T+Cy+Pr	13	4.83	47.3	0.000	1.84E+10
36	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox+Ci*Pr	15	7.04	47.5	0.000	2.03E+10
22	Ca+Ar+Hp+Ox+T+Cy+Pr	13	4.65	47.6	0.000	2.21E+10
16	Cy+Ox+T+Ox*T	10	0.98	48.2	0.000	2.96E+10
34	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox+Ci*T+Ci*Pr	16	7.83	48.2	0.000	2.98E+10
33	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox+Ci*T+Pr*Ar	16	7.58	48.7	0.000	3.81E+10
31	Ci+Ar+Hp+Ox+T+Cy+Pr+Ci*Ox	14	5.03	49.2	0.000	4.77E+10
15	Cy+Ox+T	9	-0.6	49.2	0.000	4.82E+10
20	Ar+Hp	8	-2.1	49.9	0.000	6.87E+10
12	Ci+Ox+T+Ci*Ox+Ci*T	11	0.89	50.6	0.000	9.82E+10
7	Ca+Ox+T	9	-1.6	51.1	0.000	1.27E+11
10	Ci+Ox+T	9	-1.6	51.2	0.000	1.30E+11
2	Ci	7	-4.2	52.1	0.000	2.01E+11
1	Ca	7	-4.3	52.2	0.000	2.22E+11
5	Ci+Ox	8	-3.3	52.4	0.000	2.37E+11
3	Ca+Ox	8	-3.3	52.5	0.000	2.49E+11
38	Ci+Ar+Hp+Ox+T+Cy+Al+Pr+Fi+Ci*Ox+Ci*T+ Ci*Pr+Ci*Al+Ox*T+Pr*Ar	19	9.19	52.7	0.000	2.77E+11
29	Ci+Ar+Ox+T+Cy+Pr	12	0.91	52.8	0.000	2.99E+11
21	Ca+Ar+Ox+T+Cy+Pr	12	0.75	53.2	0.000	3.49E+11
11	Ci+Ox+T+Ci*Ox	10	-1.5	53.2	0.000	3.61E+11
13	Ca+Al	8	-4.2	54.2	0.000	5.83E+11
18	Pr+Ar	8	-4.2	54.3	0.000	6.09E+11
6	Ci+Ox+Ci*Ox	9	-3.2	54.4	0.000	6.58E+11
17	Pr+Ar+Fi	9	-3.9	55.7	0.000	1.23E+12
19	Pr+Ar+Pr*Ar	10	-3.8	57.8	0.000	3.58E+12

Regression slopes. Confidence intervals of most factors included in the best model did not include zero: age, specific conductance, hydroperiod length, intraspecific competition, predation, and the interactions intraspecific competition*temperature and intraspecific competition*predation. The confidence intervals of the factors site, pond surface area, oxygen concentration, temperature and the interaction intraspecific competition*oxygen concentration included zero (Table 5).

Table 5. Regression slopes (Beta) of the best-selected model (# 26, Table 4) that was used to predict variation in body size at metamorphosis. Standard errors (SE), lower (LCI) and upper confidence intervals (UCI) are given. Factors with bold values do not include zero in 95% confidence intervals. See Table 1 for abbreviations of factors.

Code	Factor	Beta	SE	LCI	UCI
	(Intercept)	**5.239**	**0.073**	**5.096**	**5.382**
Age	Age	**0.286**	**0.017**	**0.253**	**0.319**
Ar	Pond surface area	0.094	0.058	-0.0196	0.207
Ca	Intraspecific competition	**-0.250**	**0.041**	**-0.330**	**-0.169**
Ca:Ox	Competition:oxygen	-0.046	0.030	-0.104	0.012
Ca:Pr	Competition:predation	**0.143**	**0.031**	**0.082**	**0.203**
Ca:T	Competition:temperature	**-0.141**	**0.029**	**-0.197**	**-0.084**
Cy	Specific conductance	**-0.292**	**0.058**	**-0.405**	**-0.178**
Hp	Hydroperiod length	**-0.175**	**0.055**	**-0.282**	**-0.067**
Ox	Oxygen	-0.006	0.045	-0.094	0.082
Pr	Predation	**-0.219**	**0.078**	**-0.371**	**-0.066**
Si	Site	-0.153	0.158	-0.462	0.156
T	Temperature	0.071	0.055	-0.036	0.178

Predicting variation in body size at metamorphosis. Body size at metamorphosis decreased with both increasing specific conductance (Table 5, Fig. 5a), and hydroperiod length (Fig. 5b). Size at metamorphosis increased with increasing pond surface area. The effect of intraspecific competition depended interactively both on temperature and predation risk (Figs 5c and 5d). Intraspecific competition had no effect at low temperature. At high temperature, increasing competition negatively affected body size at metamorphosis (Fig. 5c). Tadpoles metamorphosed at the largest size in ponds with low competition and low predation, and at the smallest size in ponds with high competition and high predation risk (Fig. 5d).

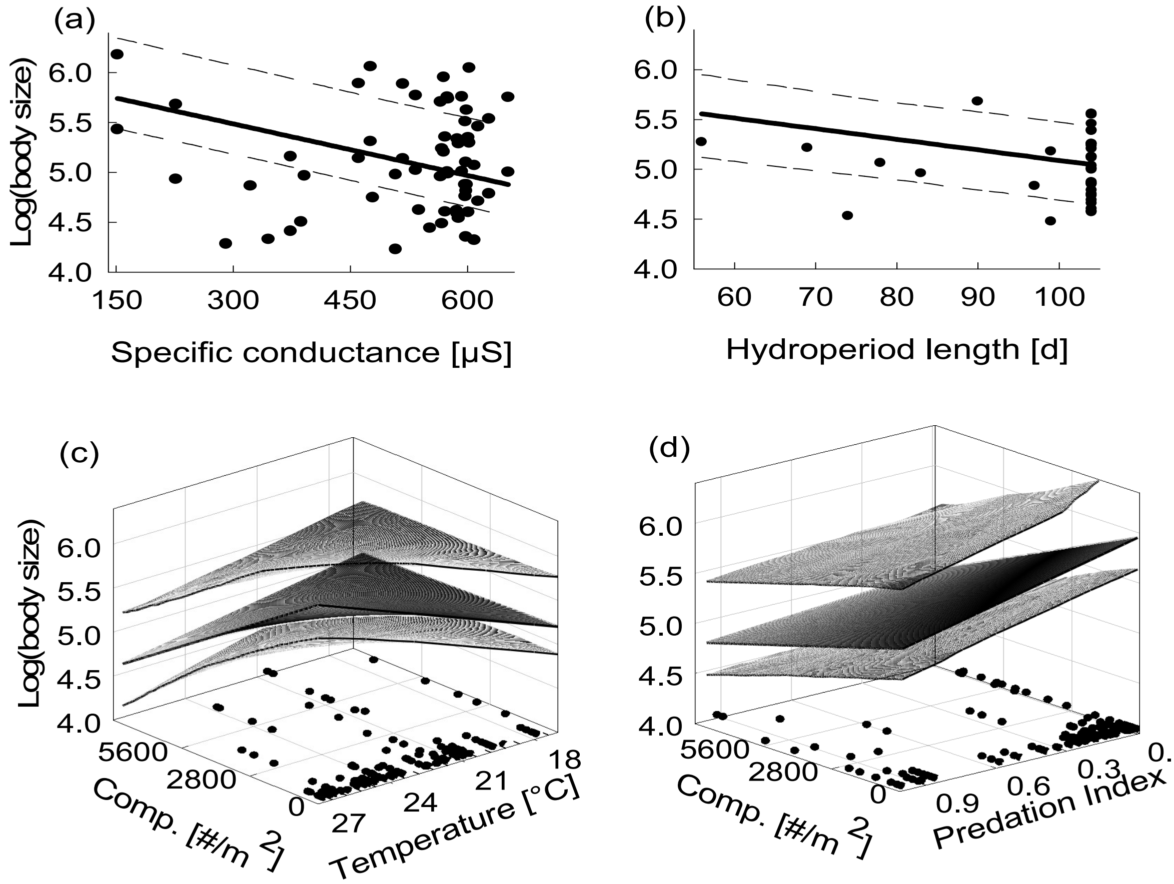

Figure 5: Predicted log-body size in relation to (a) specific conductance, (b) hydroperiod length, the (c) combined effects of intraspecific competition and temperature, and (d) intraspecific competition and predation risk. Upper and lower dashed lines (a, b), and meshs (c, d) are 95% confidence intervals. Points give the distribution of measured data. The model that best explained spatial variation in log-body size was used (Table 4). Predictions were calculated within the range of observed factor values.

Discussion

Body size at metamorphosis is a critical trait for species with complex life cycles as it affects survival and fitness later in life (Altwegg & Reyer, 2003; Berven, 1990; Smith, 1987). In amphibians, the factors that govern variation in body size at metamorphosis have been well explored by mesocosm experiments (Alford, 1999) but not under natural conditions (but see Gray & Smith, 2005; Petranka, 1984; Reading, 2003; Reading & Clarke, 1999). We asked, what are the

i) differences in larval traits (body size at metamorphosis, growth rate) and in population density at metamorphosis between the major habitats (active tract, riparian forest), and what are ii) the direct and the interactive effects of abiotic and biotic factors on among-pond variation in body size at metamorphosis?

Differences in larval traits between the two major habitats

Tadpoles from the active tract had slightly larger body size at metamorphosis (Fig. 4a), higher growth rates (Fig. 4b), and completed metamorphosis on average three weeks earlier than tadpoles from the riparian forest. Based on reaction norms for ectotherms (Berrigan & Charnov, 1994), tadpoles in the warm ponds of the active tract should metamorphose early at a small size. In the cool ponds of the riparian forest instead, tadpoles should metamorphose later at a larger size. The rule described by Berrigan and Charnov (1994) was only partly met, as slow growing tadpoles from the cool ponds tended to be smaller at metamorphosis than fast growing tadpoles from warm ponds (Table 3, Fig. 4). This pattern likely reflects differences in other environmental characteristics such as food availability and predation risk (Table 3), which apparently override the rule described by Berrigan and Charnov (1994). The better performance of tadpoles from the active tract implies higher juvenile survival in the terrestrial stage (Altwegg & Reyer, 2003; Smith, 1987). Furthermore, metamorphs from the active tract are likely to reach maturity earlier than metamorphs from the riparian forest (Altwegg & Reyer, 2003; Semlitsch, Scott & Pechmann, 1988).

Population density at metamorphosis from ponds of the active tract was about one to two orders of magnitude larger than from ponds of the riparian forest (Table 3, Fig. 4d), mainly because the overall larval mortality rate, between first sampling and metamorphosis, was 16% lower in the active tract than in the riparian forest. This implies potential for source-sink dynamics (Pulliam, 1988) with ponds in the active tract acting as sources (rate of mortality < rate of birth) and ponds in the riparian forest acting as sinks (rate of mortality ≥ rate of birth). If these patterns were consistent in the long-term, we would expect that all individuals breed in the active tract. Because of the large movement distances reported in common toads, all ponds were virtually available to all individuals (Indermaur, Schmidt & Tockner, 2008). As toads still breed in the riparian forest, there must be costs of breeding in the active tract, which were not apparent in our 1-year study. Therefore, costs may be only incurred infrequently, for example, during dry and wet years (Beebee, 1983). During dry years, ponds in the active tract may more likely run dry than ponds in the riparian forest because of the higher temperature and infiltration loss in the active tract (Fig. 3). During wet years, larvae in ponds of the active tract are at higher flooding risk while ponds in the riparian forest are less exposed to flooding. Hence, ponds of the active tract contribute to population growth only in the absence of major floods and droughts during the breeding season. Therefore, ponds in the active tract may act as alternate sinks or sources, depending on the disturbance regime, while ponds in the riparian forest contribute constantly but marginally to population growth. We may describe it as a shifting source-sink dynamics with dispersal between these spatially separated populations (Doncaster, Clobert, Doligez *et al.*, 1997). In the long term, geometric mean population fitness of these spatially separated populations may converge to the same levels. Although source-sink dynamics have been described for a variety of amphibian species (Gill, 1978; Sinsch, 1992; Trenham, Koenig & Shaffer, 2001), we conclude that long-term dynamics are necessary to correctly classify sources and sinks (Runge, Runge & Nichols, 2006; Semlitsch, Scott, Pechmann *et al.*, 1996).

Direct and interactive effects of abiotic and biotic factors on log-body size at metamorphosis

Body size at metamorphosis was maximal in large, shallow and warm ponds, with low specific conductance, low oxygen concentration, low intraspecific competition, and low predation risk (Table 5). These conditions are characteristic for ponds of the active tract, except for oxygen concentration and specific conductance, which were both higher in the active tract (Table 3).

We found strong interactive effects of intraspecific competition and temperature as well as intraspecific competition and predation risk on body size at metamorphosis (Figs 5c and 5d), in line with a number of experimental studies (Alford, 1999). Temperature largely determines the biological reaction times, thereby affecting metabolism and hence growth rates of organisms. At low temperature, body size was not affected by competition (Fig. 5a). Hence, low temperatures limited growth, indicating that in ectotherms the processing of food is determined by abiotic conditions (Angilletta, Steury & Sears, 2004). At high temperature, however, competition negatively affected body size. Resource competition therefore affects body size at and time to metamorphosis. The strength of resource competition seems to be regulated by temperature.

Predation risk and competition jointly reduced growth rates (Fig. 5d), corroborating experimental results (Van Buskirk & Yurewicz, 1998). At low competition, increasing predation risk inhibited growth rates. At high competition, body size did not decrease as strong as it did when competition was low. Hence, the joint effects of high predation risk and high competition increased growth rates. The latter pattern is likely linked to antipredator behavior. For example, feeding activity is usually lowered to reduce predatory encounters, which in turn improves resource availability (Skelly & Werner, 1990). Likewise, guppies from high-predation environments experienced higher levels of resource availability than guppies from low-predation environments (Reznick, Butler &

Rodd, 2001). Hence, antipredator-behavior and competitor densities both affect resource availability which in turn affects larval growth.

Conclusions

Our results demonstrate that tadpoles from ponds of the active tract of a dynamic floodplain performed better (larger body size at metamorphosis, higher growth rate, higher population density at metamorphosis) than tadpoles from ponds of the riparian forest. This highlights the potential for shifting source-sink population dynamics with balanced dispersal rates, primarily governed by droughts and floods. The flooding-mediated disturbance regime maintains ponds in the active tract in a state that is favorable for amphibians (Smith, 1983).

The particular contribution of this study is that it shows that metamorphic traits of populations occurring in different environments are controlled by the direct and interactive effects of abiotic and biotic factors under natural conditions. We thereby corroborate experimental findings (Alford, 1999), which is essential for the feedback loop between experimental and field studies (Werner, 1998). Furthermore, our results re-emphasize the need for long-term data on population density and distribution to understand erratic fluctuations in population size and to correctly identify source and sink habitats. Future research should explore whether differences in larval traits in these spatially separated populations are associated with adult traits and life time fitness.

Conservation implications

Our results demonstrate that ponds in the active tract are pivotal for the performance (body size at metamorphosis, growth rate) and population density of anuran larvae and hence population persistence. Large, shallow, warm, and low predation risk ponds in the active tract led to improved larval performance. The creation and maintenance of ponds in early succession stages depends on a natural river bed and flow regime and an unconstrained river morphology.

However, these ponds are among the first habitats that disappear as a consequence of flow regulation and channelization of rivers. Restorations of riverine floodplains are therefore a promising method to create and maintain habitats of early succession stages that are favorable for tadpole performance.

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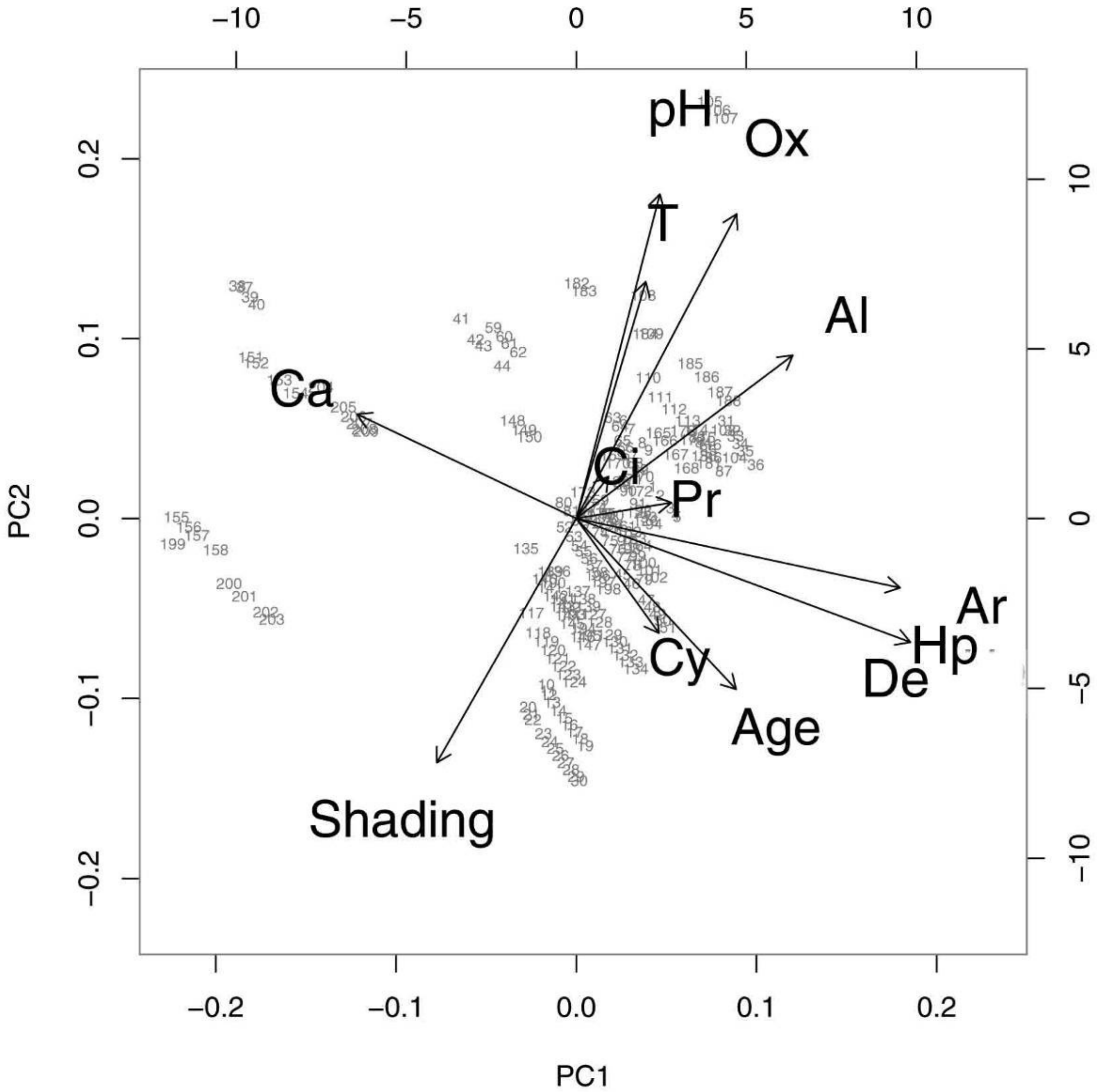
Appendix A. Results from a principal component analysis (PCA). See Table 1 for abbreviations of factors. All factors listed in Table 1 except shading were used in the PCA. Shading was constantly higher in the riparian forest than in the active tract. We used factor site (two levels: active tract, riparian forest) instead of factor "shading" in the analyses as it integrates both shading and the spatial distribution of ponds.

The factors group into components reflecting local conditions (pH, Ox, T, Al), hydromorphology (Ar, Hp, De, Cy) and pond distribution (shading). Age describes similar pond characteristics such as Cy. Factors Pr, Ci, lie between the groups local conditions and hydromorphology. Ca is inversely related to hydromorphological characteristics.



Appendix B. Correlation matrix of factors used in candidate models for predicting variation in log-body size at metamorphosis. Y=Log(Mean body size). All factors were standardized prior to calculating Pearson coefficients. *n* = number of animals. See Table 1 for abbreviations of other factors.

Factors	Y	Sh	Age	Ct	Ci	Ar	De	Hp	Al	T	Ox	Ph	Cy	Pr
Y	1.000	0.490	0.328	-0.355	-0.241	0.113	-0.080	-0.043	-0.044	0.328	0.102	0.153	0.004	-0.173
Sh		1.000	-0.164	-0.313	-0.026	0.222	0.173	0.079	0.034	0.305	0.241	0.253	-0.105	-0.010
Age			1.000	-0.365	-0.183	0.267	0.162	0.384	-0.002	-0.250	-0.044	-0.069	0.060	0.243
Ct				1.000	0.237	-0.451	-0.164	-0.370	-0.049	-0.150	-0.005	0.139	-0.443	0.101
Ci					1.000	0.063	0.094	0.109	0.030	-0.079	0.082	0.140	-0.109	0.253
Ar						1.000	0.233	0.663	0.437	0.018	0.114	-0.008	0.259	0.186
De							1.000	0.417	-0.087	0.002	-0.044	-0.049	-0.248	0.434
Hp								1.000	0.245	-0.040	0.095	-0.072	0.094	0.214
Al									1.000	0.159	0.554	0.385	0.152	0.126
T										1.000	0.316	0.316	0.093	-0.281
Ox											1.000	0.860	-0.134	0.187
Ph												1.000	-0.406	0.241
Cy													1.000	-0.556
Pr														1.000

OUTLOOK

We quantified both aquatic and terrestrial summer habitat selection of amphibians as well as the fitness-consequences of aquatic habitat selection. Our main conclusion is that differential preferences for the abiotic and biotic environment most probably occur in all life history stages of species, thus facilitating the co-existence of species with complex life cycles. However, in my thesis I did not consider habitat selection and fitness-consequences of all life history stages. For example, a) we quantified terrestrial summer habitat selection by adults but not juveniles; b) we quantified the fitness-consequences of aquatic habitat selection but not of terrestrial habitat selection; c) we neither quantified the selection of overwintering habitats by juveniles and adults nor mortality in overwintering habitats. Hence, to justify our expectation that differential habitat selection may facilitate co-existence in all life history stages, we would have to estimate habitat selection of juveniles and adults for a complete annual cycle. Moreover, to explore the fitness consequences of terrestrial habitat selection we would have to estimate juvenile and adult mortality in terrestrial habitats as well, which may be achieved by applying capture-mark-recapture methods over at least three years (Lebreton et al. 1992; Schmidt et al. 2008).

Areas for future research

Linkage between home-range dynamics and population dynamics

Further research should focus in more detail on the relationships between habitat structure, resource density, and population dynamics. A number of empirical studies have shown that home-range size depends on habitat structure and/or resource density (Buner et al. 2005; Ebersole 1980; Prohl and Berke 2001; our study). Home-range size is expected to decrease with increasing population density (Kjellander et al. 2004; Wang and Grimm 2007). Empirical evidence that both home-range size and population dynamics are similarly controlled by the interplay of habitat structure and resource density is still missing. Approaching this topic would require an experimental setup where levels of habitat structure and resource density are manipulated, and the response (home-range size, population density) can be quantified.

Variation in terrestrial home-range size and environmental unpredictability

We found that individual factors (sex, body mass, animal identity) poorly explained among-individual variation in home-range size. This result may have resulted from environmental unpredictability as theory predicts differences among individuals (e.g. differential habitat preferences, physiological state, tolerance to environmental factors, age, experience) to be more important in stable rather than in dynamic environments (Klopfer and MacArthur 1960). Future research should therefore focus on the effect of differences among individuals on home-range size in relation to environmental stability. As dynamic floodplains become more and more regulated and, therefore, habitat stability increases, we would expect differences among individuals becoming more important in controlling home-range size. In this thesis, we focussed on the ecological processes fundamental to home-range structure. Exploring home-range structure and associated fitness components in relation to varying levels of environmental stability would therefore shed more light on the evolution of home-range structure.

Habitat selection and the impact of intrinsic components

We quantified terrestrial habitat selection of two toad species across spatial scales: home-range placement within the floodplain, space use within 95% home-ranges, and space use within 50% core areas. Home-range placement was determined by the availability of habitat types while space use within 95% home-ranges and 50% core areas depended on resource availability. That home-range placement did not depend on resource availability was puzzling as the terrestrial summer habitat should provide all essential resources for individual maintenance and survival. Even more puzzling was that animals placed home-ranges in floodplain areas where prey density was higher and temperature lower than outside home-ranges. These results suggest that home-range placement can be influenced by intrinsic differences among individuals such as genetic differences, experience (age), physiological state and tolerance to environmental factors (Hutto 1985; Wecker 1964; Wiens 1972). Future studies should therefore focus in more detail on unexplained differences among individuals, for example by predicting habitat selection in relation individual age (Smirina 1994) and genetic diversity (Marshall et al. 2003) in addition to resource availability and habitat type.

Breeding site selection and environmental unpredictability

We found that differential responses to abiotic conditions and predation risk determine breeding site selection rather than avoidance of competitors. We concluded that niche-differentiation and hence local co-existence was facilitated by the typical high degree of structural organization in unpredictable environments (Tockner et al. 2006). Strong environmental gradients reflect this high degree of structuring; and natural disturbances are required to maintain these gradients and hence large variation in environmental conditions (Gallet et al. 2007). We therefore expect that environmental variation decreases with flow regulation, sediment control and morphological control. Loss of environmental variation would consequently reduce the co-occurrence of species and hence decrease local species diversity.

Local and regional co-existence

Based on our results we can clearly reject the neutral model as most species combinations were found locally co-existing in higher frequency than expected by chance. It is expected that regional diversity summarizes processes affecting local diversity. Though, other studies predicted regional species diversity accurately assuming neutral processes (Hubbell 2001; Muneepeerakul et al. 2008; Tilman 2004). Predicting the occurrence of the anuran species studied at both the local and the regional scale by assuming neutral processes and non-neutral processes, might help to clarify linkages between local and regional species diversity. For example, better prediction of regional species diversity by neutral than non-neutral processes would indicate that regional diversity is not simply conditional on local diversity.

Relevance of metamorphic traits for adult traits and life time fitness?

We found that tadpoles from the active tract of the dynamic floodplain metamorphosed earlier and tended to be at a larger size than tadpoles from the riparian forest. Moreover, the production of metamorphs was about one to two orders of magnitude larger in ponds of the active tract compared to ponds of the riparian forest. These results indicate that metamorphs from the active tract survive better in later life, have higher fecundity, and reach maturity earlier than metamorphs form the riparian forest (Altwegg and Reyer 2003; Berven 1990; Smith 1987). Future research should therefore explore whether differences in larval traits in these spatially separated populations are associated with adult traits and life time fitness.

Impact of disturbances on source-sink dynamics

Population density at metamorphosis was much larger in ponds of the active tract than in ponds of the riparian forest, implying potential for source-sink dynamics (Pulliam 1988) with ponds in the active tract acting as sources (rate of mortality < rate of birth) and ponds in the riparian forest acting as sinks (rate of mortality ≥ rate of birth). If these patterns were consistent in the long-term, we would expect that all individuals breed in the active tract. We hypothesize that population density at metamorphosis in the active tract is primarily governed by droughts and floods while predation regulates population size in the riparian forest. We expect that these spatial differences in population density at metamorphosis reflect two evolutionary strategies, resulting in similar mean geometric fitness in the long term. Similar mean geometric fitness would result because costs for breeding in the active tract can be extremely high during dry and wet years (Beebee 1983); but these costs may be incurred only infrequently. Hence, ponds of the active tract may act as alternate sinks or sources, depending on the disturbance regime, while ponds in the riparian forest contribute constantly but marginally to population growth. Thus, long-term data are necessary to correctly classify sources and sinks (Runge et al. 2006; Semlitsch et al. 1996), and to justify the presence of the two evolutionary strategies proposed.

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