(Un)sustainable use of frogs in West Africa and resulting consequences for the ecosystem

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1 Summary

Amphibian populations are declining world wide. One of the main reasons for this decline is overexploitation. All over the world many frog species are caught from the wild, mainly for food, but also for medicinal purposes or pet trade. Herein I report first investigations from West Africa. Whereas particular West African tribes have always used frogs as food, medicine or for cultural reasons, a current increase in frog hunting seems to be new. With a continuously growing human population and a simultaneous decline of protein resources such as fish the exploitation of amphibians is likewise increasing. Consequently, amphibian declines are likely and may result in measurable changes of aquatic and riparian ecosystems. In the beginning of my thesis, I will provide an overview on exploitation and trade of amphibian species in different regions of the world, with a main emphasis on West Africa, and on possible resulting consequences for the ecosystem.

In Africa the use, mainly consumption, of different frog species has not been in the focus of scientific research yet. By carrying out interviews with frog-collectors, market-women and consumers in Burkina Faso, Benin and Nigeria I was able to quantify and evaluate the use and trade of frogs in these countries. In Burkina Faso the frog trade mainly took place on a local scale, whereas in northern Benin and Nigeria, I detected an intensive cross-border trade of amphibians. Frogs, predominantly the African Tiger Frog, *Hoplobatrachus occipitalis*, was collected in the North of Nigeria and neighbouring countries, and were subsequently traded into the cities of southern Nigeria. It is likely that the amount of traded frogs is not sustainable in some areas, partly already resulting in declining frog populations.

As part of my investigation ethnozoological data on the use of frogs by local ethnic groups (Mossi, Gourmanché, Yoruba and Hausa) were additionally collected. Different catching methods, ways of preparation, and applications as medical treatments were recorded and are discussed. Therewith I could reveal the importance of amphibians for local culture, and in particular for consumption, medical treatments and West African livelihoods. The frog trade in West Africa definitely needs more attention and detailed investigation to avoid frog declines and ecosystem consequences.

In the second part of my study I examined possible consequences of declining amphibian species for the remaining amphibian community and the ecosystem. Here, I concentrated on potential consequences of the loss of larval anurans for aquatic ecosystems. Tadpoles show various feeding strategies. Depending on the species, tadpoles are filter feeders, herbivorous, detritivorous, or even carnivorous. Depending on the trophic level a species belongs to, this particular species may play an important functional role for the ecosystem and respective ecosystem processes. Many tadpoles for example are filter-feeders and play an important role in maintaining water quality. Declining tadpole numbers could thus result in eutrophication of ponds. In rural savanna regions of West Africa, freshwater ecosystems are essential water resources for humans and their livestock. Altering these ecosystems therefore may have important economic and health consequences.

Moreover, changes and losses in the amphibian community can have prospective impacts on water chemistry, algae and aquatic invertebrate taxa. Concerning the latter one, I focused on the impact on mosquito larvae, which constitute prey and competitors of tadpoles. Especially the tadpoles of the foremost consumed species, *H. occipitalis*, are carnivorous and potentially feed on mosquito larvae. A decrease of *H. occipitalis* tadpoles might hence result in an increase of mosquitoes. Since mosquito species transmit diseases, this can also negatively affect humans or cattle (for example, mosquitoes of the genus *Anopheles* transmit the parasite *Plasmodium* sp., the pathogenic agent of Malaria). Finally the harvested adults usually devour large quantities of insects, amongst them pest species. All these ecosystem services are lost when the frogs are harvested in an unsustainable manner.

In an empiric approach I conducted a survey of natural freshwater ponds in two study regions in Burkina Faso. I compared ponds situated in different disturbance regimes: ponds in and around villages, where frogs were collected for consumption, and in protected areas, where frog harvest was prohibited. For each pond tadpole species composition, habitat parameters and presence and absence of mosquito larvae species were recorded. A multiple analysis revealed various connections between different communities and ecosystem factors, with an emphasis on habitat parameters and mosquito assemblages. Species richness was lower and species composition differed in anthropogenic disturbed areas. Altered habitat factors and spatial effects were mainly responsible for these differences. However, harvesting of adult amphibians could have affected tadpole composition and occurrences of particular species as well. I especially detected a low rate of occurrences of tadpoles of *H. occipitalis* in anthropogenic disturbed areas. These tadpoles, however, are top-predators in food webs of freshwater ponds and could have further affected occurrences and abundance of remaining tadpole species. Altered tadpole assemblages could have further affected mosquito assemblages and correlations between both assemblage compositions have indeed been detected. In the disturbed areas where the carnivorous *H. occipitalis* tadpoles showed a very low frequency of occurrence, filter-feeding tadpole species simultaneously occurred more often. These species are direct competitors of filter-feeding mosquito larvae as for example larvae of *Anopheles*. Accordingly, *Anopheles* larvae were recorded comparatively less often in disturbed areas. The harvest of *H. occipitalis* may thus have a positive impact regarding humans since consequently there may be less Malaria transmitting *Anopheles* mosquitoes around villages.

I could show that tadpole species composition was definitely altered in freshwater ponds in disturbed areas. As these ecosystems also offer services for the local human population a better understanding of its functioning is important. This includes the ecological roles, which its inhabitants such as tadpoles play to evaluate the effect of their potential loss.

In addition to the empiric approach I thus conducted an experimental approach to investigate the ecological role of four functionally different tadpole species (*H. occipitalis*, *Kassina fusca*, *Ptychadena bibroni*, *Phrynomantis microps*) and the consequences of their losses for pond ecosystems. Therefore, artificial ponds (mesocosms) were set up, in which tadpole assemblages of varying species composition were combined. The effects of the presence or absence of a particular tadpole species on survival, growth, development and trophic position of the remaining species of this tadpole community, on specific parameters of water quality and on mosquito larvae assemblages were tested. All four tadpole species differed in their trophic position within a pond's food web. The experimental approach revealed various complex interactions between the focus species. Intraspecific isotope signatures in some species varied according to the respective tadpole assemblages. Community composition was especially important for the tadpoles' survival. The carnivorous tadpoles of *H. occipitalis* have been proven to be top-predators in pond food webs. Their presence and absence respectively, extremely affected survival rates of the co-occurring tadpole species. Furthermore, interactions between prey species, in particular density effects, in the absence of the top predator also mattered and growth and development of specific species changed depending on species composition. Most parameters of water quality were not affected by species exclusion, but I detected an important influence of *P. microps* on water transparency. Mosquitoes occurring in the artificial ponds were mostly *Anopheles gambiae* s.l. and *Aedes vittatus*. However, interactions of the four different tadpole species with mosquito larvae were not detected in the experiment and larvae densities seemed not to be affected by tadpole's presence or exclusion. Rather abiotic factors such as water depth affected their densities. However, interactions between mosquito larvae and tadpoles in natural ponds cannot be excluded.

All examined tadpole species differed in their ecological roles; hence the loss of just one species can have crucial consequences for ecosystem processes and thus for ecosystem functions in general. In the end of my thesis I provide a number of recommendations for further research activities and for necessary steps in controlling the frog trade to prevent overexploitation and its consequences for the ecosystem.

1.1 Zusammenfassung

Amphibien sind weltweit von einem Artenrückgang betroffen. Vermutlich ist einer der wesentlichen Gründe für diese Entwicklung die übermäßige Ausbeutung bestimmter Froscharten. In vielen Regionen der Welt werden Frösche aus ihrem natürlichen Lebensraum entnommen, vorwiegend um sie als Nahrungsmittel zu nutzen, aber auch für medizinische Anwendungen und im internationalen Tierhandel.

Die Untersuchungen zur vorliegenden Arbeit geben erstmals Einblicke in Form, Umfang und Auswirkungen der extensiven Nutzung von Fröschen in Westafrika, wo bestimmte Ethnien traditionell Frösche zur Ernährung, als Heilmittel oder für kulturelle Zwecke verwenden. Die zu beobachtende exzessive Ausbeutung verschiedener freilebender Populationen dürfte dagegen neu sein. Ihre stetige Zunahme scheint mit der kontinuierlich wachsenden Bevölkerung Westafrikas und dem gleichzeitigen Rückgang anderer Nahrungsressourcen wie Fisch zu korrelieren. Folglich ist schon aufgrund dieser Situation mit einem Rückgang betroffener Arten zu rechnen. Die Frage, in wie weit sich daraus messbare Veränderungen in den betroffenen Ökosystemen ergeben, soll mit der vorliegenden Arbeit beantwortet werden.

Die Nutzung von Fröschen in Westafrika, war bisher nicht Gegenstand wissenschaftlicher Untersuchungen. Deshalb war es zunächst das Ziel dieser Arbeit, Interviews mit Froschfängern, Marktverkäufern und Konsumenten in den westafrikanischen Ländern Burkina Faso, Benin und Nigeria durchzuführen. Die damit gewonnenen Erkenntnisse, ermöglichten die Nutzung und den Handel von Fröschen zu quantifizieren und zu bewerten. Während der Froschhandel in Burkina Faso eher auf lokaler Ebene abläuft, ließ sich im Norden von Benin und in Nigeria ein intensiver grenzüberschreitender Handel mit Fröschen nachweisen. Dabei erwies sich der westafrikanische Tigerfrosch, *Hoplobatrachus occipitalis*, sowohl im Norden Nigerias als auch in den angrenzenden Nachbarländern als die mit Abstand meist gefangene Art, welche zur weiteren Verwertung in die großen Städte Südnigerias transportiert wird. Mit hoher Wahrscheinlichkeit ist dieser Froschhandel in einigen Gebieten nicht mehr nachhaltig und mit sinkenden Amphibienpopulationen ist zu rechnen.

Ergänzend konnten ethnozoologische Daten der Froschnutzung innerhalb der verschiedenen lokalen Ethnien, wie Mossi, Gourmanché, Yoruba und Hausa, ermittelt werden. In diesem Kontext stehen unterschiedliche Fangmethoden, Zubereitungsarten und Heilanwendungen, die in dieser Arbeit beschrieben und diskutiert werden. Die umfangreichen Untersuchungen zu dieser Arbeit geben Aufschluss über die Bedeutung von Fröschen in der Kultur, der Heilkunde, aber insbesondere für die Ernährung und den Lebensunterhalt der Menschen in den Studiengebieten.

Der Froschhandel in Westafrika bedarf einer größeren Beachtung und weiterer Detailuntersuchungen, um Rückgängen von Froschpopulationen und den daraus

resultierenden Konsequenzen für die betroffenen Ökosysteme und für die Bevölkerung dieser Region begegnen zu können.

Die Untersuchungen zum zweiten Teil dieser Arbeit dienten der Ermittlung möglicher Auswirkungen von Artenrückgängen auf Amphibiengemeinschaften und betroffene Ökosysteme. Zur Realisierung dieses Vorhabens wurden temporäre Savannangewässer in Burkina Faso gewählt, um auf Kaulquappenebene Artenverluste und die sich daraus ergebenen Konsequenzen zu studieren. Entsprechend der Wahl ihrer Nahrungsstrategie lassen sich Kaulquappen u.a. in Filtrierer, Herbivore, Detritivore und Karnivore differenzieren. Je nach Zugehörigkeit einer trophischen Gilde, übernehmen Kaulquappen eine wichtige funktionelle Rolle in ihrem Ökosystem, was für bestimmte ökosystemische Prozesse bedeutsam ist. Viele Kaulquappen sind zum Beispiel Filtrierer und spielen so eine wichtige Rolle für die Aufrecherhaltung der Wasserqualität. Ein Rückgang dieser Amphibienlarven könnte daher eine Eutrophierung der betroffenen Gewässer nach sich ziehen. In den ländlichen Savannenregionen Westafrikas sind natürliche Gewässer notwendige Frischwasserquellen für die Menschen und ihr Vieh. Eingriffe und Veränderungen dieser Ökosysteme können aus diesem Grund ökonomische wie auch gesundheitliche Folgen haben.

Auch können Änderungen und Verluste in der Kaulquappengemeinschaft einen Einfluss auf die Wasserchemie, die Algengemeinschaften und die Gemeinschaften von aquatischen Invertebraten haben. In Bezug auf letzteres habe ich speziell den Einfluss auf Moskitolarven, die wiederum Beute und Nahrungskonkurrenten von Kaulquappen sind eingehend untersucht. Gerade die Kaulquappen der durch Fang und Handel besonders betroffenen Art *H. occipitalis*, sind karnivor und ernähren sich unter anderem von Moskitolarven. Ein Rückgang dieser Larven könnte daher zu einem Anstieg von Moskitos führen. Moskitos der Gattung *Anopheles* sind Überträger des Malaria auslösenden Parasiten *Plasmodium* sp. Aufgrund dieses infektiösen Potentials, müsste eine Zunahme dieser Moskitoart u.a. als äußerst problematische Entwicklung für den Menschen bewertet werden. Auch adulte Frösche ernähren sich in großen Mengen von Insekten, auch Pestarten. Diese wichtigen Ökosystem Leistungen würden verloren gehen, wenn Frösche in größeren Mengen aus ihrem natürlichen Lebensraum entnommen würden und dadurch betroffene Ökosysteme in ihrer Nachhaltigkeit empfindlich gestört wären.

Zur Klärung dieses Sachverhalts galt es im Rahmen eines empirischen Ansatzes Freilandstudien an natürlichen Gewässern in zwei Untersuchungsgebieten in Burkina Faso durchzuführen, wobei innerhalb eines Studiengebietes Gewässer miteinander verglichen wurden, die in Gebieten mit unterschiedlichem Störungsgrad lagen: Tümpel in oder in der Nähe von Dörfern mit Froschfang (gestörtes Gebiet), gegenüber Tümpeln in geschützten Gebieten mit Froschfangverbot (ungestörtes Gebiet).

Zunächst mussten von jedem Tümpel die vorherrschende Artengemeinschaft von Amphibien- und Moskitolarven und Habitatparameter ermittelt werden. Mit Hilfe multivariabler Analysen konnten Unterschiede in den Beziehungen zwischen verschiedenen Gemeinschaftskombinationen und Ökosystemfaktoren aufgedeckt werden. Generell konnte in den anthropogen gestörten Gebieten ein niedrigerer Artenreichtum mit gleichzeitig veränderter Zusammensetzung der Artengemeinschaften konstatiert werden. Für viele dieser Unterschiede waren in erster Linie in Ausprägung und/oder Konzentration veränderte Habitatfaktoren und räumliche Effekte verantwortlich. Aber auch das Fangen adulter Frösche kann Grund für veränderte Kaulquappengemeinschaften sein. Speziell der Rückgang von *H. occipitalis* Larven in gestörten Gebieten könnte das Vorkommen und die Abundanzen der übrigen Quappenarten stark beeinflussen da sie als Top-Predatoren der betroffenen Nahrungsnetze identifiziert wurden. Eine veränderte Quappengemeinschaft kann zudem einen Effekt auf die jeweils vorkommenden Moskitolarven ausüben. In den gestörten Gebieten, wo *H. occipitalis* Kaulquappen nur noch selten vertreten waren, kamen andere Arten, wie bestimmte Filtrierer, häufiger vor. Diese sind direkte Nahrungskonkurrenten von ebenfalls filtrierenden Moskitolarven, wie z.B. der Gattung *Anopheles*. In den gestörten Gebieten wurden vergleichsweise weniger *Anopheles* Larven nachgewiesen. Demnach hätte der Fang von *H. occipitalis* Fröschen unter Umständen sogar eine für den Menschen positive Auswirkung, indem als Konsequenz weniger Malariaübertragende *Anopheles* Mücken in den Dörfern vorkommen.

Die Verluste von Froscharten und die möglicherweise daraus resultierenden Konsequenzen zu kennen, ist für ein besseres Verständnis der betroffenen Ökosysteme, speziell der ökologischen Rolle betroffener Arten im System essentiell, auch mit Blick darauf, in wie weit solche Veränderungen für den Nutzen der Menschen in der Region vertretbar sind.

Zur Aufklärung dieser Zusammenhänge wurde ergänzend zu den empirischen Studien ein Artenausschlussexperiment durchgeführt. Dazu wurde die ökologische Rolle von vier Kaulquappenarten mit jeweils unterschiedlicher Nahrungsstrategie (*H. occipitalis*, *Kassina fusca*, *Ptychadena bibroni* und *Phrynomantis microps*), und die Konsequenzen ihres Verlustes für das Ökosystem ermittelt. Damit die Untersuchungen unter kontrollierten und wiederholbaren Bedingungen erfolgen konnten, wurden künstliche Gewässer (Mesokosmen) mit Kaulquappengemeinschaften in unterschiedlicher Kombination angelegt. So war es möglich die Effekte von An- bzw. Abwesenheit einzelner Kaulquappenarten auf das Überleben, das Wachstum und die Entwicklung sowie die trophische Position der restlichen Kaulquappen zu untersuchen. Gleichzeitig ließ sich so feststellen, wie sich die jeweiligen Konstellationen auf bestimmte Wasserqualitätsparameter und die Moskitolarvenzusammensetzung auswirken. Die vier Kaulquappenarten unterschieden sich in ihrer trophischen Position im Nahrungsnetz. Der experimentelle Ansatz konnte zudem komplexe Interaktionen zwischen den vier Fokusarten aufdecken. Intraspezifische Isotopensignaturen variierten in einigen Arten in Abhängigkeit der jeweiligen Artenzusammensetzung. Diese wiederum war für das Überleben der Quappen besonders wichtig. Ausschlaggebend für Wachstum und Entwicklung der Beutearten waren neben der Anwesenheit karnivorer *H. occipitalis* Kaulquappen auch Interaktionen zwischen den Beutearten selbst. Die Mehrzahl der Wasserparameter zeigte sich von den jeweiligen Artenausschlüssen unbeeinflusst. Der Filtereffekt von *P. microps* Larven auf die Wassertrübung stellte dabei eine Ausnahme dar. In den künstlichen Gewässern dominierten Moskitolarven der Art *Anopheles gambiae* s.l. und *Aedes vittatus*. Zwischen ihnen und den verschiedenen Kaulquappenarten ließen sich keine Interaktionen nachweisen, auch nicht im Bezug auf die Larvendichte der beobachteten Moskitoarten. Diese variierte eher mit abiotischen Habitatfaktoren in den untersuchten Gewässer wie z.B. Wassertiefe. Mögliche Interaktionen zwischen Moskitolarven und Kaulquappen ließen sich dagegen in natürlichen Gewässern nicht ausschließen.

Die vier untersuchten Kaulquappenarten unterschieden sich in ihrer ökologischen Rolle. So kann der Verlust nur einer einzigen Art essentielle Konsequenzen für ökosystemische Prozesse und damit für die Ökosystemfunktion haben. Da im Rahmen der empirischen Studie Unterschiede in der Artenzusammensetzung in den unterschiedlichen Störungsgebieten nachgewiesen wurden und speziell in den gestörten Gebieten einige Arten bzw. sogar ganze Gattungen nicht gefunden wurden ist anzunehmen, dass die im Experiment vorgefundenen Konsequenzen von Artenausschlüssen auch im Freiland so oder ähnlich eintreffen. Empfehlungen für zukünftige Forschungsarbeiten aber vor allem für wichtige Schutz- und Kontrollmaßnahmen zur Vermeidung einer Übernutzung von Froscharten und der daraus resultierenden negativen Effekte für Ökosysteme werden abschließend in dieser Dissertation genannt.

1.2 Résumé

Les populations d'amphibien régressent à travers le monde et la surexploitation constitue l'une des raisons principales de ce déclin. Un peu partout, de nombreuses espèces de grenouilles sont capturées dans leur milieu naturel pour être mangées mais aussi pour servir de préparations médicinales ou pour alimenter le commerce animal. Ce travail de thèse rapporte quelques investigations réalisées en Afrique de l'Ouest. Bien que certaines tribus d'Afrique de l'Ouest se servent depuis longtemps des grenouilles pour l'alimentation, la préparation de médicaments ou pour des raisons culturelles, on observe actuellement une augmentation de la chasse aux grenouilles qui semble correspondre à un phénomène nouveau. Avec la croissance continue de la démographie humaine et la diminution simultanée des ressources protéines comme des poissons, l'exploitation des amphibiens augmente également. Par conséquent, on peut s'attendre à un déclin progressif des amphibiens qui risque d'entrainer des modifications sensibles des écosystèmes aquatiques et riverains.

Au début de cette thèse sera présenté un aperçu d'ensemble de l'exploitation et du commerce des espèces d'amphibiens dans les différentes régions du monde, avec une attention toute particulière pour l'Afrique occidentale, et de leurs conséquences éventuelles sur les écosystèmes.

Jusqu'à présent, l'utilisation de différentes espèces de grenouilles en Afrique, principalement pour l'alimentation, n'a été que peu étudiée d'un point de vue scientifique. Le commerce et l'utilisation des grenouilles au Burkina Faso, au Bénin et au Nigeria ont été quantifiés et évalués via des entrevues avec ceux qui collectent les grenouilles, les femmes qui les vendent sur les marchés et ceux qui les consomment. Au Burkina Faso, le commerce de grenouilles avait principalement lieu à l'échelle locale tandis qu'au nord du Bénin et au Nigeria, le commerce d'amphibiens était à la fois intensif et transfrontalier. Les grenouilles, tout particulièrement la grenouille de l’Adrar Atar, *Hoplobatrachus occipitalis*, étaient recueillies dans le Nord du Nigeria et dans les pays voisins avant d'être vendues dans les villes du sud du Nigeria. La quantité de grenouilles vendues est telle qu'elle ne semble pas viable dans certaines régions où on observe déjà un déclin partiel des populations de grenouilles.

Dans le cadre de cette enquête éthno-zoologique, certaines des données recueillies concernaient également l'utilisation faite des grenouilles par des groupes ethniques locaux (Mossi, Gourmanché, Yoruba et Haoussa). Ainsi, différentes méthodes de capture, différents modes de préparation et d'applications dans les traitements médicaux ont été enregistrés et sont discutés dans ce travail. Cela permet de révéler l'importance que les cultures locales accordent aux amphibiens, tout particulièrement dans l'alimentation, dans les traitements médicaux et aussi comme moyen de subsistance en Afrique de l'Ouest. Si nous souhaitons éviter un déclin des espèces de grenouilles, ainsi que les conséquences écologiques qui en découlent, il est impératif de prêter davantage d'attention au commerce de grenouilles en Afrique de l'Ouest et d'étudier de plus près ce phénomène.

Dans la deuxième partie de cette étude, ce sont les conséquences possibles de la diminution des espèces d'amphibiens sur les populations restantes et sur les écosystèmes qui ont été examinées. Dans ce contexte, une attention toute particulière a été accordée aux conséquences potentielles de la diminution des larves d'anoures sur les écosystèmes aquatiques. Les têtards manifestent différentes stratégies d'alimentation et, selon les espèces, ils se nourrissent par filtration, sont herbivores, détritivores ou même carnivores. En fonction du niveau trophique auquel appartient une espèce, les têtards peuvent exercer un rôle fonctionnel essentiel sur les écosystèmes et sur les processus écosystémiques. Par exemple, de nombreux têtards se nourrissent par filtration et jouent un rôle important dans le maintien de la qualité de l'eau. Par conséquent, la diminution du nombre de têtard pourrait entraîner l'eutrophisation des étangs. Dans les régions rurales de savanes d'Afrique de l'Ouest, les écosystèmes d'eau douce constituent des ressources en eau essentielles tant pour les humains que pour leurs bétails. Toute modification apportée à ces écosystèmes risque donc d'entraîner des conséquences économiques et sanitaires importantes.

De plus, toute modification ou perte au sein des populations d'amphibiens peut affecter ensuite la chimie de l'eau, les algues et les divers invertébrés aquatiques. À ce propos, une attention toute particulière a été portée sur l'impact des larves de moustiques, lesquelles constituent à la fois les proies et les concurrents des têtards. Cela concerne plus particulièrement les têtards de l'espèce, *H. occipitalis*, l'espèce la plus consommée par l'homme, qui présentent un régime alimentaire carnivore et qui se nourrissent peut-être de larves de moustiques. Une diminution du nombre de têtards de *H. occipitalis* pourrait donc entraîner une augmentation du nombre moustiques. Sachant que certaines espèces de moustiques transmettent des maladies, une augmentation de leurs nombres risque d'affecter les populations humaines ou leurs bétails (par exemple, les moustiques du genre *Anopheles* qui transmettent le parasite *Plasmodium* ; l'agent pathogène du paludisme). Enfin, les spécimens adultes qui sont récoltés mangent une grande quantité d'insectes, parmi lesquels des espèces nuisibles. Ainsi, lorsque la collecte de grenouilles s'opère sous un mode non durable, ce sont tous ces services écosystémiques qui sont perdus.

Une étude empirique a également été menée pour comparer les étangs d'eau douce naturelle soumis à différent régimes de perturbations dans deux régions du Burkina Faso ; les étangs situés dans et autour des villages, là où les grenouilles sont collectées pour être mangées par rapport aux étangs situés dans des zones protégées, là où la collecte de grenouilles est interdite. Pour chacune des compositions d'espèces de têtards relative à chaque étang, les paramètres d'habitat et la présence/absence de larves d'espèces de moustiques ont été enregistrés. Une analyse multiple a révélé la présence de connexions diverses entre les différentes communautés et les facteurs de l'écosystème, et plus particulièrement entre les paramètres de l'habitat et les assemblages de moustiques. Dans les zones perturbées par la présence humaine, la richesse en espèces était plus faible et la composition en espèces était différente. Les principaux responsables de ces différences étaient les facteurs d'habitats modifiés et les effets spatiaux. Toutefois, il est également possible que la collecte d'amphibiens adultes ait influencé la composition des têtards et la présence d'espèces particulières. Dans les régions perturbées par l'homme, l'occurrence des têtards de l'espèce *H. occipitalis* était moins importante. Cependant, ces têtards sont des supra-prédateurs de la chaîne alimentaire des étangs d'eau douce et il est possible qu'ils aient davantage affecter l'occurrence et l'abondance d'autres espèces de têtards. Les assemblages altérés de têtard pourraient avoir affecté davantage les assemblages de moustiques et des corrélations entre les compositions d'assemblage ont en effet été détectées. Dans des zones perturbées, en les têtards carnivores de *H. occipitalis* ont montre une fréquence de l’occurrence très bas, l’occurrence des têtards que se nourrissent par filtration étaient simultané plus haut. Ces espèces sont des compétiteurs directes des larves de moustique que se nourrissent par filtration, comme par exemple les larves de *Anopheles*. En conséquence, des larves des *Anopheles* étaient référencer comparativement plus rare dans des zones perturbées. Pour cette raison le récolte de *H. occipitalis* pourrait avoir un impact positive en rapport des humains parce qu’en suite il y aurait moins des moustiques de *Anopheles* qui peuvent transmettre le Malaria dans des villages.

Ainsi, dans les étangs d'eau douce des zones perturbées, la composition des espèces de têtards était très clairement touchée. Sachant que ces écosystèmes sont également bénéfiques pour les populations autochtones, il est essentiel d'en connaître mieux son fonctionnement. Cela comprend les rôles écologiques joués par ses habitants, tels que les têtards, afin d'évaluer les conséquences de leur perte potentielle.

En plus de l'approche empirique précédemment abordée, une approche expérimentale a également été réalisée pour étudier le rôle écologique de quatre espèces de têtards différent d'un point de vue fonctionnel (*H. occipitalis*, *Kassina fusca*, *Ptychadena bibroni*, *Phrynomantis microps*) et les conséquences de leurs pertes sur les écosystèmes des étangs. Des étangs artificiels (mésocosmes), dans lesquels des assemblages de têtards de différentes compositions d'espèces étaient combinées, ont été réalisés. Les effets de la présence ou de l'absence d'une espèce particulière de têtard sur la survie, la croissance, le développement et la position trophique des autres espèces de cette communauté de têtard, et sur des paramètres spécifiques liés à la qualité de l'eau et aux assemblages de larves de moustiques, ont été testés. Il s'agit de quatre espèces de têtards qui diffèrent dans leurs positions trophiques au sein de la chaîne alimentaire d'un étang. L'approche expérimentale a révélé l'existence de diverses interactions complexes entre les espèces ciblées. Des signatures isotopiques intraspécifiques chez certaines espèces variaient selon les assemblages de têtard respectifs. La composition de la communauté était particulièrement importante pour la survie des têtards. Les têtards carnivores de *H. occipitalis* se sont avérés être de supra-prédateurs dans la chaîne alimentaire des étangs. Leur présence et leur absence ont respectivement affecté de manière importante les taux de survie des espèces de têtards co-occurrentes. En outre, des interactions entre les espèces proies, en particulier les effets de densité, en l'absence du prédateur étaient également importants et la croissance et le développement de certaines espèces changeaient en fonction de la composition des espèces. La plupart des paramètres liés à la qualité de l'eau n'ont pas été touchés par l'exclusion des espèces. Cependant, une influence importante de *P. microps* sur la transparence de l'eau a été détectée. Les principaux moustiques observés dans les étangs artificiels étaient *Anopheles gambiae* s.l. et *Aedes vittatus*. Toutefois, aucune interaction entre les quatre espèces différentes de têtards et les larves de moustiques n'a été détectée dans cette expérience tout comme les densités de larves ne semblaient pas non plus être affectées par la présence ou l'absence de têtards. Des facteurs abiotiques comme la profondeur de l'eau sont probablement le plus influé de leurs densités. Néanmoins, ces résultats ne peuvent exclure la possibilité d'interactions entre les larves de moustiques et les têtards dans les étangs naturels.

Toutes les espèces de têtard étudiées différaient dans leurs rôles écologiques; ainsi la perte d'une seule espèce peut avoir des conséquences cruciales sur les processus des écosystèmes et donc, sur le fonctionnement général de l'écosystème. Pour conclure, diverses recommandations relatives aux activités de recherche et aux mesures à prendre dans le contrôle du commerce de grenouilles pour prévenir la surexploitation et ses conséquences sur les écosystèmes, sont fournies à la fin de ce travail de thèse.

2 Background

2.1 Global exploitation of frogs with a focus on West Africa

The human reliance upon natural resources is often seen as one of the strongest political arguments to preserve the global biodiversity (CBD 2008). However, an over-exploitation of these resources is one of today's major threats to biodiversity, leading e.g. to habitat degradation and conversion, erosion of genetic diversity, species decline and loss, destabilization and destruction of ecosystems and hence is jeopardizing present and future livelihoods (COWLISHAW et al. 2005, CBD 2008).

Amphibians are one of the most threatened groups of animals, with approximately one third of known species being endangered (STUART et al. 2004). Reasons for this are numerous but besides habitat degradation and loss, disease and enigmatic declines; over-exploitation is mentioned as one of the main causes (GIBBONS et al. 2000, STUART et al. 2004, HALLIDAY 2008). Whereas habitat destruction, global change and most of all disease gained much research interest, overexploitation of frogs is rarely mentioned to be of any importance. However, a recent report by NIASSE et al. (2004) states that utilization is the main threat for 281 amphibian species, 54% of these being already listed as Vulnerable, Endangered or Critically Endangered. The results of the Global Amphibian Assessment support this statement by listing 220 amphibian species that are currently used for food, already indicating that many more species might be affected (COX et al. 2008). Amphibian species are harvested and used worldwide mainly as a food source, i.e. frog legs are thought to be delicacies in many regions of the world. However, frogs are also collected for leather production and souvenirs, for the pet trade and for cultural reasons including traditional medicine (OZA 1990, VEITH et al. 2000, STUART et al. 2004, YOUNG et al. 2004, KUSRINI & ALFORD 2006, GONWOUO & RÖDEL 2008). Most attempts to commercially breed frogs in larger quantities under artificial, farm-like conditions have failed (OZA 1990, HELFRICH et al. 2001) and hence the majority of amphibians are still taken directly from the wild (HELFRICH et al. 2001, KUSRINI & ALFORD 2006).

Where this exploitation exceeds sustainability amphibian species are doomed with local declines or extinctions (JENSEN & CAMP 2003). In addition to these direct impacts on particular species, other indirect effects like the loss of ecosystem functions are likely consequences (DUFFY 2002, WRIGHT 2006). For example, amphibians play an important role in various terrestrial and aquatic ecosystems, both as predators and as prey (TOLEDO et al. 2007, HALLIDAY 2008). A decline of particular amphibian species may thus result in an overabundance of prey species, i.e. various pest arthropods, and/or leave predators with a limited food supply. From our long-term personal experience it seems that the use of particular frog species recently dramatically increased in West Africa. The consequences are unknown. In this paper we will summarize the most prominent examples of over-exploitation in amphibians worldwide. We provide a first insight into the West African situation and we highlight potential ecological and socioeconomic consequences and thus respective research needs.

2.1.1 Unsustainable use of amphibians

Although many amphibians species are adopted to large mortality rates and hence to moderate exploitation alike, an intensive harvest at least of particular species, may result in an over-exploitation of local population or even whole species and thus in their decline. However, hard data on actual harvested frog numbers and respective consequences for populations are still scarce or completely lacking. In table 2.1 we provide information on the main frog and salamander species harvested, including their respective uses. In the following paragraphs I briefly summarize amphibian exploitations in different areas of the world. We mainly focus on the use of frogs for consumption. Besides food trade, particular amphibians are also caught in larger quantities for the pet trade (SCHLAEPFER et al. 2005). The most demanded species is the African dwarf clawed frog (*Hymenochirus curtipes*; 2.4 million individuals officially imported into the US between 1998 and 2002), followed by the Chinese fire-bellied newt (*Cynops orientalis*, app. 1.6 million) and the Oriental fire-bellied toad (*Bombina orientalis*, app. 1 million; SCHLAEPFER et al. 2005). About 13 000 poison-dart frogs (Dendrobatidae) were exported from South and Latin America between 1987 and 1993, the majority, nearly 8000 individuals, being imported into the US (GORZULA 1996). A total of 221 000 frogs of different species (app. 70% Mantella spp.) were exported from Madagascar for the international pet market between 2000 and 2006 (CARPENTER et al. 2007).

Europe.- Frogs were already consumed during the Roman Empire, and presumably much earlier. Since the 16th century frogs and their legs in particular, have became a delicacy in European gastronomy (NEVEU 2004). The majority is harvested from nature. In smaller quantities this was sustainable for centuries. However, after the Second World War the demand seemed to have increased tremendously. The European green frog complex, *Pelophylax* spp. in particular, has served as the main resource for frog legs especially in France, followed by Belgium and the Netherlands (responsible for 80% to 90% of the European trade). Due to the large numbers of harvested frogs in France (40 to70 tons (t) per year, NEVEU 2004) the collecting, transport and sale of native frog populations became prohibited by French law in 1980 (NEVEU 2004). As a consequence France has today's highest import rates of frog legs (3000 t to 4000 t per year) and living frogs (700 t to 800 t per year, NEVEU 2004) from countries in Southeast Asia (compare VEITH et al. 2000). A more recent example from autochthonous frog use in Europe is from Romania (TÖRÖK 2003). As fish stocks declined drastically in the Danube Delta a sustainable exploitation of frogs was proposed. Between 1960 and 1970 an annual amount of 120 t of frogs were collected from Romanian waters, resulting in many depopulated biotopes that previously were crowded with frogs.

Asia.- Asian countries currently export the highest numbers of frogs. Until 1985, 200 million frogs were exported each year from Asia to Europe, e.g. West Germany imported 500 t (12 million frogs) from Bangladesh in 1984 (OZA 1990). For many years India and Bangladesh were the main Asian exporters for frog legs. However, as a consequence of declining frog populations (mainly *Hoplobatrachus tigerinus* and *Euphlyctis hexadactylus*), and a resulting increase of insect pests, India banned exportation in 1985 (OZA 1990). Unfortunately there seem to be no study examining potential recovery of these species since.

With 4000 t of frogs harvested annually (KUSRINI & ALFORD 2006), Indonesia is today's world's leading export country for frog legs, most of them (83.2%) still sold to Europe. Because of limited supplies, particularly during the dry season, the export numbers sometimes do not even meet the demand. Established frog farms are not cultivating native species, but introduced species like the North American bullfrog, *Lithobates catesbeianus* (KUSRINI & ALFORD 2006). If these frogs make their way into the wild, this might be a further threat to the native fauna. Bullfrog larvae are known to have strong negative effects on the growth and survival rate of tadpoles of other species (KUPFERBERG 1997, KIESECKER et al. 2001), and adults regularly devour other amphibian species (FICETOLA et al. 2007). Furthermore *Lithobates catesbeianus* is a successful carrier of chytridomycosis (DASZAK et al. 2004), an infectious disease of amphibians caused by the fungus *Batrachochytrium dendrobatidis*.

Indonesian frogs are however, not only harvested for the overseas market, the local market seems to play an equal or even greater role (KUSRINI & ALFORD 2006). As the human population grows and resources like fish decline, people often switch to other protein sources like particular frog species, mainly larger ranids. Recent investigations have shown that in Indonesia large frogs have already completely disappeared from habitats such as paddy fields and river sides close to human settlements, where they usually should be common (VEITH et al. 2000). Depleted frog populations due to over-exploitation seem to be a common Southeast Asian phenomenon. In China, 84 species are negatively affected by utilization, because of illegal collecting and a high domestic demand for these species. Especially ranid species, like *Hoplobatrachus rugulosa*, are harvested for utilization. Twelve out of 39 utilized species decline rapidly and are threatened with extinction (CARPENTER et al. 2007). The collapse of populations of favourite frog leg species in Asia shows that even in common, fast-growing and fecund species such levels of exploitation are not without limit (LAU et al. 2008).

Table 2.1. The table lists (in alphabetic order) the most exploited amphibian species (excluding dendrobatid frogs), the scale of trade (R= regional, N= national, I= international), and the current conservation status based on IUCN Red List (LC= Least Concern, VU= Vulnerable, NT= Near Threatened, EN= Endangered, CR= Critically Endangered).

Species	Utilisation	Region	Scale	Time of exploitation	IUCN Status	Reference
Ambystoma dumerilii	Food, medicine	Mexico	I	Present	CR	Carpenter et al. 2007
Ambystoma mexicanum	Food, medicine, pet trade, research	Mexico	I	Present	CR	Carpenter et al. 2007
Astylosternus spp.	Food	Cameroon	R	Present	LC-CR	Gonwouo & Rödel 2008
Bombina orientalis	Pet trade	East Asia	I	Present	LC	Schlaepfer et al. 2005
Chaunus arenarum	Research	Argentina	N	Present	LC	Young et al. 2004
Chaunus arunco	Research	Chile	I	Present	LC	Young et al. 2004
Chaunus marinus	Food, souvenir, pet trade, research	America, Australia	R, N, I	Present	LC	Pough et al. 2001
Conraua crassipes	Food	Cameroon	R	Present	LC	Gonwouo & Rödel 2008
Conraua goliath	Food	Cameroon	R	Present	EN	Gonwouo & Rödel 2008
Conraua robusta	Food	Cameroon	R	Present	VU	Gonwouo & Rödel 2008
Cynops orientalis	Pet trade	China	I	Present	LC	Schlaepfer et al. 2005
Euphlyctis hexadactylus	Food	India, Bangladesh	I	Past	LC	Oza 1990, Veith et al. 2000
Fejervarya cancrivora	Food	Indonesia	R, I	Present	LC	Veith et al. 2000, Kusrini & Alford 2006, Carpenter et al. 2007

Table 2.1. continued

Species	Utilisation	Region	Scale	Time of exploitation	IUCN Status	Reference
Hoplobatrachus occipitalis	Food	Africa	R, N	Present	LC	Pers. obs.
Hoplobatrachus rugulosus	Food	South and Central China	R, N, I	Present	LC	Carpenter et al. 2007, Jensen & Camp 2003
Hoplobatrachus tigerinus	Food	Southern Asia, India	I	Present	LC	Pough et al. 2001, Oza 1990, Carpenter et al. 2007
Hyla cinerea	Pet trade	United States	I	Present	LC	Schlaepfer et al. 2005
Hyla eximia	Pet trade	Mexico	I	Present	LC	Carpenter et al. 2007
Hymenochirus curtipes	Pet trade	DRCongo	I	Present	LC	Schlaepfer et al. 2005
Kassina decorata	Food	Cameroon	R	Present	LC	Gonwouo & Rödel 2008
Limnonectes macrodon	Food	Indonesia	R, I	Present	VU	Kusrini & Alford 2006, Carpenter et al. 2007
Lithobates catesbeianus	Food	North America		Present	LC	Pough et al. 2001, Carpenter et al. 2007
Lithobates pipiens	Food, research	North America	R, N, I	Present	LC	Jensen & Camp 2003
Mantella spp.	Pet trade	Madagascar	I	Present	LC-CR	Carpenter et al. 2007
Pachymedusa dacnicolor	Pet trade	Mexico	I	Present	LC	Carpenter et al. 2007
Pelophylax lessonae	Food	Europe	N, I	Present	LC	Jensen & Camp 2003
Pelophylax nigromaculata	Food	Central and Northeast China	R, N	Present	NT	Carpenter et al. 2007

Table 2.1. continued

Species	Utilisation	Region	Scale	Time of exploitation	IUCN Status	Reference
Pelophylax ridibundus	Food, medicine, research	Europe	R, N, I	Present	LC	Pough et al. 2001, Jensen & Camp 2003, Neveu 2004, Carpenter et al. 2007
Pyxicephalus adspersus	Food, pet trade	Africa	R, N	Present	LC	Pers. obs., Pough et al. 2001, Carpenter et al. 2007
Rana aurora	Food	North America	R, N	Past	NT	Jensen and Camp 2003
Rana chensinensis	Food, medicine	Central and Northeast China	R, N, I	Present	LC	Carpenter et al. 2007
Rana plancyi	Food	Central and Northeast China	R, N	Present	LC	Carpenter et al. 2007
Rana temporaria	Food	Europe	N, I	Past	LC	Neveu 2004
Telmatobius culeus	Food (human & animals), medicine, leather	Peru, Bolivia	R, N	Present	CR	Angulo 2008
Telmatobius marmoratus	Food, medicine	Peru	R	Present	VU	Angulo 2008
Trichobatrachus robustus	Food, cultural purpose	Cameroon	R, I	Present	LC	Gonwouo & Rödel 2008
Xenopus amieti	Food	Cameroon	R	Present	NT	Gonwouo & Rödel 2008
Xenopus laevis	Research, food	Africa	R, I	Present	LC	Weldon et al. 2007

America.- Whereas frogs were probably used as food by many Indian tribes for long time, it was the European immigrants introducing the commercial utilization of frogs in North America. Native frogs became important food sources and between the late 1800s and early 1900s amphibians were exploited for the American frog leg market. During this period, hundreds of thousands of red-legged frogs (*Rana aurora*) and over 20 million leopard frogs (*Lithobates pipiens* and allied species) were collected annually from California wetlands and northwestern Iowa (GIBBONS et al. 2000). It has been estimated that between 1920 and 1992 amphibian populations in an Iowa county declined from at least 20 million to 50 000. At least one-third of this decline could be attributed to harvesting; two-thirds however were due to wetland drainage (LANNOO et al. 1994). As local populations started to decline, frog legs have been imported from Asia, e.g. in 1976 2500 t of frog legs were imported to the USA, predominately from Japan and India.

It seems that some South American indigenous people were always familiar with the use of frogs. Frogs of the genus *Telmatobius* have traditionally been consumed or used for medicinal and ritual purposes by locals in the Andes of Peru and Bolivia. Their medicinal use locally varies, comprising treatment of asthma, epilepsy, headaches, and stress (ANGULO 2008). Today, the overall numbers of consumed *Telmatobius* increases and populations of different species (e.g. *T. arequipensis*, *T. coleus*, *T.gigas*, and *T. jelskii*) are declining dramatically (IUCN 2008). In Peru, dealers were selling about 180 frogs on one market in Cusco, every day (ANGULO 2008). Each week between 1200 and 2400 frogs are thus requested per dealer. Thus, besides agricultural practices and water pollution, commercial utilization is one of the main reasons for many members of this genus being severely threatened (DE LA RIVA & LAVILLA 2008).

Several American frogs were also collected for research and teaching purposes. Especially leopard frogs were harvested during the 1960s and 1970s in the US. In South America thousands of *Chaunus arunco* in Chile and *C. arenarum* in Argentina were collected for science and education (YOUNG et al. 2004). Today, more than 1000 t of amphibians and reptiles still pass the US border each year, 96% of it for commercial purposes (SCHLAEPFER et al. 2005). The consequences for the respective source populations and ecosystems are unknown.

Africa.- For research and medical purposes the African clawed frog (*Xenopus laevis*) has been used since the 1930s. In South Africa each year over 10 000 of these frogs are collected from the wild and exported to over 30 different countries since 1998 (WELDON et al. 2007). The four major suppliers for *Xenopus laevis* in South Africa are restricted to collect only in certain areas and during specific time periods to prevent over-exploitation. However, it has been hypothesized that *X. laevis* is a successful carrier of chytridiomycosis and that the international trade in this species might have introduced this fungal disease to other regions of the world (IUCN 2008). In general the African frog trade and especially the actual dimension of frog harvest and consumption has not yet been a topic of scientific investigation.

In some regions amphibians (mainly toads) are used for medical treatments by villagers (e.g. south-eastern Guinea and Benin). Children's cough, appendicitis or skin injuries are some diseases treated with toads. However, in Africa most amphibians are collected for food. The consumption of larger frog species like *Pyxicephalus adspersus*, *P. edulis*, *Hoplobatrachus occipitalis*, *Trichobatrachus robustus*, *Conraua* spp. or *Ptychadena* spp. is known from a wide range of African countries e.g. Benin, Burkina Faso, Cameroon, Côte d'Ivoire, Ghana, Guinea, Namibia, Nigeria, South Africa and Togo (OKEYO 2004, GONWOUO & RÖDEL 2008, own data). A variety of different ethnic groups from West Africa, e.g. the Gourmanché and Mossi in Burkina Faso (Fig. 2.1), the Yacouba in Côte d'Ivoire, the Bakossi in Cameroon, and the Hausa in Nigeria, traditionally use frogs as food or for medical and cultural reasons. African amphibians are mainly harvested and consumed in and around the villages and often there is only little selection for particular species other than size, i.e. larger species preferred. Even toads (Fig. 2.2, *Amietophrynus maculates*, *A. regularis*) and tadpoles are harvested, prepared and sold on local markets.

On the Obudu plateau, Nigeria, we observed a very intense collection of frogs and their tadpoles from small rivers. This traditional use of frogs seems to have become unsustainable in recent years. Women harvesting these species now have to walk much longer distances than previously to arrive on rivers that still provide enough amphibians to make the harvest feasible (M.-O. Rödel, unpubl. data). A similar situation has been recently reported from nearby Cameroon (GONWOUO & RÖDEL 2008). Harvesting the larval stage in addition to adults may lead to a much faster breakdown of populations than collecting adults only, as this could result in an even more substantial loss of juvenile recruitment. Besides a mainly local or national trade market, we also detected larger cross-border trade of amphibians from northern Benin into Nigeria. Especially *Hoplobatrachus occipitalis* is harvest and traded in huge quantities. During one season one collector caught a minimum of 0.9 t of *H. occipitalis* from a maximum area of only 20 m² along the river banks of the Niger River, where the frogs accumulate during the dry season. With the beginning of the rains *H. occipitalis* usually migrate far into the savanna (SPIELER & LINSENMAIR 1998), the frog collection therefore not only affecting the area along the rivers, but huge parts of the hinterland. In Burkina Faso we detected commercial frog trade in some regions (province of Ganzourgou), whereas in other regions (province of Gourma) frogs are rather harvested for self-supply. Judging from interviews with villagers and colleagues (i.e. Prof. Dr. A. THIOMBIANO, Laboratoire de Biologie et Ecologie Végétale, Université de Ouagadougou, personal communication) it seems that in. the province of Gourma, the hot phase of frog

Figure 2.1. Market-woman offering fried *Hoplobatrachus occipitalis* as snack at a market in Southern Burkina Faso.

Figure 2.2. Mossi woman preparing toads (*Amietophrynus maculates* and *A. regularis*) for sale in southern Burkina Faso. The toads are beheaded, skinned, disembowelled, washed and cut into pieces before being dried. These toads are the harvest of one day.

harvest is already over, due to declining populations of *H. occipitalis* and other frog species. Comparable West African ecosystems are still rich in amphibians and all frogs from these regions so far tested for chytridiomycosis have been found to be chytrid negative (C. WELDON & M.-O. RÖDEL, unpubl. data). The frog declines in south-eastern Burkina Faso hence seem to be at least mainly driven by human collectors.

2.1.2 Economic consequences of over-exploited frog populations

Frogs play a vital role in eradicating insect pests. These pests destroy crops and carry diseases. One of the few studies estimating the effects of frog species removal from the wild was done in India (ABDULALI 1985). An adult *Hoplobatrachus tigerinus* devours approximately 10% of its own weight in insects every day. During illegal exports of Indian frog legs, 9000t of *H. tigerinus* were harvested annually. Hence, 900t of insects, including mosquitoes and agricultural pests, survived daily and instead had to be controlled by other means, such as insecticides (ABDULALI 1985). The commercial frog exploitation and resulting decline thus resulted in an increased use of agrochemical products in rice paddies, lead to increased environmental pollution and needed higher financial investment to achieve harvests comparable to the previous ones. Thus in summary the frog leg trade resulted in minor economic gains in form of foreign exchange, but simultaneously lead to major ecological and economic losses (OZA 1990). Unfortunately, similar studies are lacking for most parts of the World including Africa.

In West Africa, the arid and semi-arid regions in the Sahel and Sudanian zones are already affected by climate change (DE WIT & STANKIEWICZ 2006). Alterations in rainfall patterns, increasing droughts, and decreasing availability of open waters will strike local human populations as well as wildlife. Unreliable and shrinking crops, however, do lead towards increasing dependence on and use of natural resources. Under this scenario, it is unlikely that the demand for amphibians will diminish in the near future. In case of a potential overexploitation of particular frog species effects on the respective ecosystem may be inevitable (LAU et al. 2008). In the next section I will summarize which effects potentially may result from declining frog populations.

2.2 Declining amphibian populations and the consequences for the ecosystem

A stable ecosystem maintains its characteristic diversity of major functional groups, its productivity, and rates of biogeochemical cycling despite predictable or unpredictable natural disturbances. However, an altered biodiversity may affect ecosystem properties and there might be a point at which alterations will adversely affect ecosystem functions and potentially even human welfare (DAILY et al. 1997, LOREAU et al. 2001, HOOPER et al. 2005, DOBSON 2006). Studies investigating the ecological role of amphibians indicate that, along with the inherent tragedy of these losses, amphibian declines will likely result in measurable effects to aquatic and riparian ecosystems. Today, many amphibian species are threatened with serious population declines (HOULAHAN et al. 2000, STUART et al. 2004). Increasing pressure from habitat degradation, fragmentation and alteration, commercial overexploitation, invading exotic species, (UV)B radiation, chemical contaminants and the pathogenic fungus, *Batrachochytrium dendrobatides*, which causes chytridiomycosis, are defined as the main causes for their declines (HALLIDAY 2008, LIPS et al. 2008). Currently one in three amphibian species are threatened with extinction (STUART et al. 2004). This loss may have serious and deleterious ecological effects and will constitute not only a significant loss to global biodiversity but also the loss of a variety of direct benefits to humans (TYLER et al 2007).

Larval amphibians live in freshwater habitats where they are important primary and secondary consumers, and even predators. If they are lost directly (e.g. due to agrochemical products) or indirectly (removal of adults) impacts on algal assemblages and primary production (e.g. OSBORNE & MCLACHLAN 1985, WILBUR 1997, RANVESTAL et al. 2004), sediment dynamics and seston quality (e.g. RANVESTAL et al. 2004), and other aquatic fauna (e.g. mosquito larvae) are likely (BLAUSTEIN & CHASE 2007). For rock-pools in Malawi it has been shown that tadpoles play a major role in transferring nutrients from sediment particles to the water column, where they become available to planctonic and epineustic algae (OSBORNE & MCLACHLAN 1985). The abundant adult consumers of invertebrates and the herbivorous tadpoles furthermore serve as food for a variety of predators, such as dragonfly larvae, water beetles and bugs, turtles, snakes, birds and mammals (WAGER 1965, HEYER & MUEDEKING 1996, MCCOLLUM & LEIMBERGER 1997, MCDIARMID & ALTIG 1999, RÖDEL 1999, POULIN et al. 2001, KOPP et al. 2006, TOLEDO et al. 2007).

In tropical ecosystems amphibians often occur in vast abundances, e.g. African puddle frogs, *Phrynobatrachus*, occur in high abundances in forest (ERNST & RÖDEL 2006) and savanna ecosystems (BARBAULT 1967, GARDNER et al. 2007). In a swampy valley in central Ivory Coast BARBAULT (1972) recorded up to 1453 *Phrynobatrachus* per hectare. RÖDEL (1998) counted tadpole (up to 20 species) densities of up to 30.7 individuals per litre in temporary

West African savanna ponds. In a shallow pond, not a drying up one, he detected more than 1,200 tadpoles per m². Declining tadpole numbers will therefore most likely result in changing energy and nutrient cycles and e.g. changes of water chemistry may be expected.

However, in order to understand the significance of these losses and their actual consequences more quantitative and qualitative information on the ecological roles of amphibians and their different ontogenetic stages is urgently needed (WHILES et al. 2006). Here, we summarize some of the more likely consequences of anuran species loss in a particular environment. Our main emphasis is on the aquatic larval stage, which comprises various functional groups of ecological importance to freshwater systems (e.g. carnivore, herbivore, detritivore, filter feeding, or suspension feeding tadpoles; MCDIARMID & ALTIG, 1999).

2.2.1 Ecological consequences...

Tadpoles, many of which are primary consumers, have been shown to profoundly influence ecosystem structure and function by altering algal assemblages, patterns of primary production, and organic matter dynamics in a variety of freshwater habitats (e.g. KUPFERBERG 1997, FLECKER et al. 1999). However, up to date, only a handful of manipulative field studies have shown that primary production, nutrient cycling, and invertebrate populations change when tadpoles are removed or reduced in numbers (OSBORNE & MCLACHLAN 1985, LAMBERTI et al. 1992, FLECKER et al. 1999, KIFFNEY & RICHARDSON 2001, RANVESTAL et al. 2004).

2.2.1.1 …on water quality

Ecologists have always been interested on how abiotic factors affect living organisms. Many studies have analyzed how amphibians are affected by different chemicals, hence by water quality. But reciprocal effects likewise exist. Most anuran larvae are filter-feeders (MCDIARMID & ALTIG 1999), playing an important ecological role in the maintenance of water quality. Filtering activity is often so high, that the complete volume of many water bodies is turned over in short time (OSTROUMOV 2005), e.g. a maximum filter feeding capacity of 770 millilitres (ml) filtered water per gram (g) per minute (min) was detected for *Xenopus laevis* tadpoles (VIERTEL 1992).

SEALE (1980) reported that tadpoles are able to reduce natural eutrophication by reducing rates of primary production, i.e. tadpoles reduce nitrogen input into the aquatic system by cutting down the biomass of nitrogen-fixing blue-green algae and by exporting nitrogen assimilates from the aquatic to the terrestrial environment via metamorphosis. Tadpoles are even able to remove bacteria from water. To sustain on such a diet, tadpoles have to filter every few minutes a water volume that equals their own body (SANDERSON & WASSERSUG

1990). A decline of tadpoles might therefore easily result in eutrophication of ponds. This was reported for temperate regions (SEALE 1980), but may be of even larger importance in tropical aquatic ecosystems (OSBORNE & MCLACHLAN 1985, RÖDEL 1998). Gaining knowledge about the different aspects of ponds' water quality regulation may be essential, especially in tropical savanna regions where temperate waters are of extreme value for the local populations and their cattle (Fig.2.3.). Unfortunately and despite their importance for humans, little research has been done on the ecology and function of tropical ponds.

Figure 2.3. Water from temporary ponds is used by the human population in Burkina Faso.

2.2.1.2 …on algal vegetation

Tadpoles' growth rates are often limited by the availability of phytoplankton (JOHNSON 1991). In reverse tadpoles foraging behaviour and activity are influencing phytoplankton growth (WILBUR 1997). Tadpole exclusion experiments are a valuable method to investigate tadpoles' effect on algae in aquatic ecosystems. By using this approach, FLECKER et al. (1999) detected that tadpoles significantly reduced the periphyton biomass in an Andean stream. This effect became stronger with increasing tadpole density. Roughly speaking, by feeding on periphyton and associated organic sediments, tadpoles clean up the bottom. In upland Panamanian streams RANVESTEL et al. (2004) could show that diatoms were significantly more abundant and species rich on tiles in enclosures, than on tiles where tadpoles had access to. Grazing and bioturbating tadpoles had the potential to transform assemblages of tall, stalked and erect or loosely attached algae, into a more cropped assembly of closely attached and low growing species, that were able persist under the grazing pressure. It is further possible that tadpoles grazing on periphyton may set free nutrients for the phytoplankton, and phytoplankton grazers may set free nutrients for the periphyton. A severe reduction of tadpoles will thus significantly increase algal biomass, alter algal assemblage structure and increase the accumulation of organic and inorganic sediments on the substratum (RANVESTEL et al. 2004).

2.2.1.3 …on other grazing species

Many studies examined density dependent effects on tadpole growth and development (e.g. ADOLPH 1931, ALFORD 1989, WILBUR 1997, FLECKER et al. 1999, BLAUSTEIN & CHASE 2007). High densities of intra- and interspecificly competing tadpoles can lead to slower growth rates, longer time to metamorphosis, lower mass at metamorphosis and a higher overall mortality rate (FLECKER et al. 1999, RUDOLF & RÖDEL 2007). Similarly, tadpoles can also affect other grazers or filter feeder such as dipteran larvae (MCLACHLAN 1981, KNIGHT et al. 2004). While sometimes tadpoles actually increase the access to food, which is usually not available to dipteran larvae (MCLACHLAN 1981), in most interactions tadpoles negatively affect them (BLAUSTEIN & MARGALIT 1994, 1996, MOKANY & SHINE 2002a, b). Hence, a loss of anuran larvae will entail a competition release in favour of larval dipterans.

…like on mosquitoes.- Adult, blood sucking mosquito females often are vectors for human diseases, such as malaria, yellow fever etc. Hence, knowledge about factors affecting their abundances is important for human welfare. During the 1990s a series of outdoor experiments were undertaken in the Negev Desert, Israel, to examine the interaction between mosquito larvae (*Culiseta longiareolata*) and tadpoles of the green toad (*Bufo viridis*; BLAUSTEIN & MARGALIT 1994, 1995, 1996). They revealed that both species feed on periphyton and co-occur in very high densities. When tadpoles and invertebrate larvae started their development simultaneously they competed strongly, but symmetrical. However, if one species started development earlier, the more advanced larvae acted as intraguild predators and preyed on the other species' larvae. So, early-stage *Culiseta* larvae are vulnerable to predation by *Bufo* tadpoles. MOCKANY & SHINE (2003a, b) carried out further experiments on the interactions between mosquitoes and tadpoles in Australia. They detected that survival rate and adult wing size of *Culex quinquefasciatus* and *Ochlerotatus australis* were significantly reduced in the presence of competing tadpoles. This kind of knowledge could play an important role in mosquito control, as wing size can affect mosquito longevity and the ability to reproduce. The mechanisms behind this phenomenon are not clearly understood. Fungi in the tadpoles' faeces may act as growth inhibitors. It is clear however, that mosquito larvae are strongly affected by their interactions with tadpoles. The

presences of competitors predominantly affect growth and development, but hence indirectly may also affect survival rates. Mosquito and anuran larvae often act on the same trophic levels. Many *Anopheles* and *Culex* larvae are primarily filter feeders, consuming phytoplankton while many *Aedes* and *Culiseta* mosquito larvae are primarily periphyton feeders (STAV et al. 2005, MATTHYS et al. 2006, BLAUSTEIN & CHASE 2007) (Fig. 2.4).
Hence, anuran and controphic dipteran larvae usually compete with each other and may both alter algal assemblages and biomass.
Some tadpoles are not only competing with mosquito larvae, but are acting on a higher trophic level as mosquito predators. This e.g. especially concerns the very effectively hunting tadpoles of the African *Hoplobatrachus occipitalis*. However, these carnivorous tadpoles hunt other tadpoles alike (RÖDEl 1998, SPIELER & LINSENMAIR 1998) and thus reduced numbers of these predators may result in higher densities of other tadpole species and consequently may increase competitive pressure on mosquito larvae. Declining populations of i.e. *H. occipitalis*, which is harvested in huge quantities (see above), may thus very differently effect mosquito populations.

Figure 2.4. Mosquito larvae feeding on periphyton in a small rock pool, Benin.

2.2.2 Human health consequences declining frog populations

In terms of incidence rate and mortality caused by vector-borne disease, mosquitoes are the most dangerous animals confronting mankind with socio-economical and political consequences, and thus threatening more than two billion people in tropical and subtropical regions. Malaria caused by the protozoans *Plasmodium* spp. and transmitted by *Anopheles* spp., affects more than 100 tropical countries with 90% of infected people living in tropical Africa. The enormous total loss of lives, the treatment costs, lost labour and resulting negative impact of the disease on the development, makes malaria a major social and economic burden. In Africa malaria generates annual costs of almost 12 billion US$, slowing the continents economic growth by 1.3% per year (WHO 2004). In addition to malaria, arboviruses like the yellow fever, dengue 1-4, West Nile virus, which are transmitted by *Aedes* spp., and filariosis, caused by nematodes and transmitted by *Culex* spp. and *Mansonia* spp. are causing major health problems as well.

Former studies have shown that, malaria transmission is usually higher in rural than in urban areas (STAEDKE et al 2003). There it is also more likely to find mosquitoes larvae co-occurring with tadpoles in temporary ponds (MATTHYS et al. 2006). The number of adult mosquitoes is largely regulated by abiotic and biotic factors such as predation, parasitism, competition and food (BARRERA et al. 2006). Despite the well known negative effects on biodiversity, it has been reported that mosquito numbers decreased following the arrival of cane toads in the Caribbean, Papua New Guinea, and Australia (HAGMAN & SHINE 2007). HAGMAN & SHINE (2007) postulated that cane toad tadpoles, reducing sizes of female mosquitoes, may reduce the insects' disease-carrying potential as smaller mosquitoes have lower fitness and are less likely to transmit significant diseases to humans.

Although data are rare it seems clear that tadpoles play an important role in acting on mosquito population dynamics and regulating quality of stagnant waters worldwide. To understand and predict the direct and indirect effects of amphibian over-exploitation is hence an urgent research need.

3 Dimension and first evaluation of the use and trade of amphibians in West Africa

3.1 Introduction

The use of natural resources is a strong political argument to preserve biological diversity (CBD 2008). However, overexploitation of these resources is also one of the major threats to biodiversity (COWLISHAW et al. 2005, CBD 2008), e.g. overexploitation is mentioned as one of the reasons for the worldwide amphibian decline (STUART et al. 2004, 2008). Recently, WARKETIN et al. (2009) summarized alarming data on numbers of Asian frogs collected for human consumption. In many countries frogs have always been collected on a local scale as an essential source of animal protein (ANGULO 2008, MOHNEKE et al. 2009). However, during the past decades frogs became an important international trading item. By the end of the 1990s the international frog leg trade involved more than 30 countries and in 1998 was valued worth app. 48.7 million US dollars (TEIXEIRA et al. 2001). As 95% of the traded frog legs originated from wild populations, there is growing concern over declining amphibian populations (WARKETIN et al. 2009), including potentially severe economic and social impacts (MACE & REYNOLDS 2001).

As a consequence of decreasing frog populations the collection of frogs from the wild became prohibited in various European countries (NEVEU 2004, OZA 1990). India and Bangladesh subsequently became the world’s leading producers and exporters of frog legs (TEIXEIRA et al. 2001). However, due to growing evidence that frog declines caused increasing agricultural pests and mosquitoes’ numbers, these countries banned the collection and trade of frogs. Then and until now Indonesia became the worlds main exporter for frog legs, followed by China, Taiwan and Vietnam (TEIXEIRA et al. 2001, KURSINI 2005). The local Asian frog trade was often believed to be sustainable (KUSRINI & ALFORD 2006). However, the actual numbers of harvested frogs and the socioeconomic importance of this harvest are usually unknown. This also concerns other parts of the World. In Africa amphibians are used e.g. for medical treatment or cultural reasons (e.g. PAUWELS et al. 2003, GONWOUO & RÖDEL 2008), but their importance as human food has so far not been investigated.

The human population in Africa has doubled during the past twenty years (UNPD 2009) and their need for resources has consequently resulted in an increasing rate of wildlife exploitation (MACE & REYNOLDS 2001). African wildlife was traditionally regarded as a valuable community asset, which was used and protected by customs and taboos. Today, traditions and taboos are often weakened or have disappeared, and the wildlife they previously protected is now exposed to serious threats (NTIAMOA-BAIDU 1987). Recently we got aware of a dramatically increasing demand for frogs in several West African countries.

The dimension and the actors within this frog market were unknown. The present study is the first investigating the current situation of this frog market. Based on interviews compiled in three West African countries, namely Burkina Faso, Benin and Nigeria, I aimed to get an overview of the actual amount and status of the frog collection, use and trade, as well as the socio-economical value of this market.

3.2 Methods

The study was conducted in Burkina Faso, Benin and Nigeria, West Africa (Fig. 3.1). One main focus was onto two regions in Burkina Faso; the province of Gourma, and the province of Ganzourgou. Gourma comprises an urban community, Fada N'Gourma, five rural communities and a total of 231 villages.

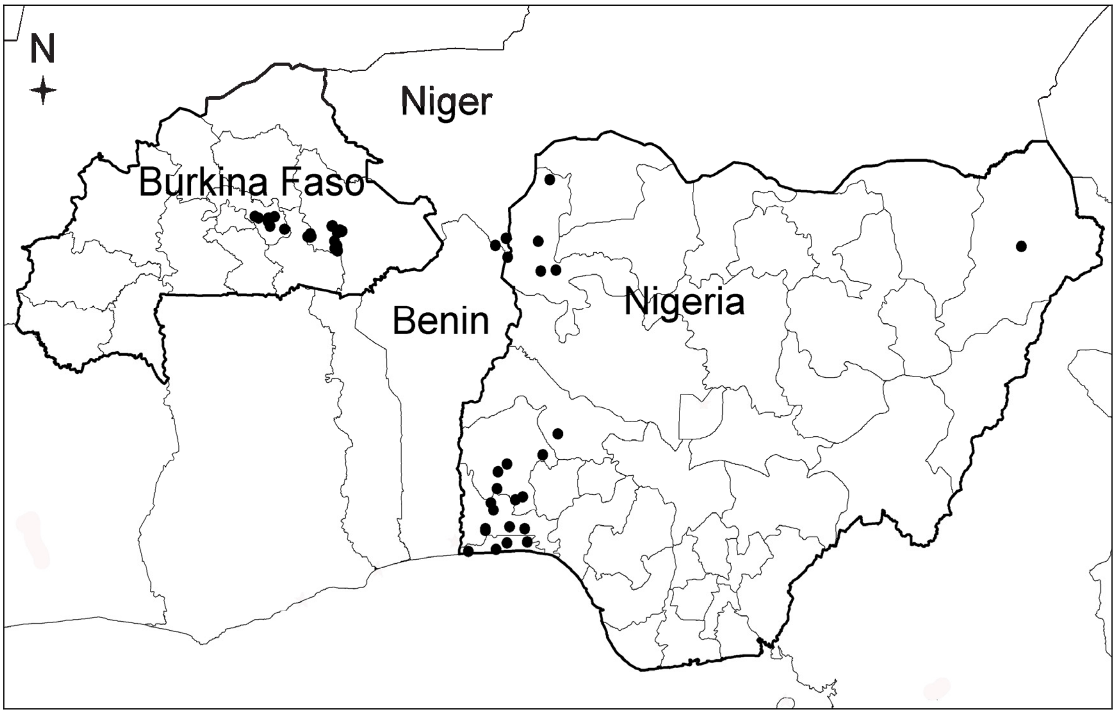


Figure 3.1. Map of the study sites in Burkina Faso and amphibian trading spots in Nigeria. Each black dot refers to a village or town where interviews have been carried out. Malanville in Benin was included as a major trading spot for frogs going into the Nigerian food market.

The human population was estimated to be 272 974 in 2006. Ganzourgou includes an urban community, Zorgho, seven rural communities, 185 villages and about 36 969 households (INSD 2006). Burkina Faso has only little natural resources, often poor, depleted soil, and a high unequal distribution of income, resulting in poor economic prospects. About 90% of the population is engaged in subsistence agriculture.

The second focus of this study was on north-eastern Benin and Nigeria. In 2007 I observed that large numbers of frogs were collected in Malanville a city in the north-east of Benin, close to the border of Nigeria and Niger. These frogs were exported into Nigeria. We followed the trade route into Nigeria and conducted interviews with a main focus onto the collecting points and trading spots in the Nigerian north-west, Kebbi state, and the larger cities and towns in south-western Nigeria (states of Ogun, Oyo, Lagos).

I developed eight semi-quantitative structured questionnaires (see appendix 1). In Burkina Faso three questionnaires were applied, one for villagers, one for market-women, and one for fishermen. In Malanville a slightly modified questionnaire was applied for the fishermen. These questionnaires were in French. In Nigeria, four questionnaires were applied; one for frog collectors, one for traders, one for market-salespersons and one for customers. These questionnaires were in English. To avoid communication problems I carried out all interviews with the help of assistants speaking the local languages.

Table 3.1. Overview on numbers, geographic origin and frog related occupations of the interviewees.

State/Place	Burkina Faso		Benin	Nigeria				Total
	Gourma	Ganzourgou	Malanville	Kebbi	Oyo	Ogun	Lagos	
Villagers	86	43						129
Market-Salesperson	5	19		5	6	3	5	43
Fishermen/ Collectors		22	7		17	12	3	61
Traders				5	10	8		23
Customers				5	8	4	3	20
Total	91	84	7	15	41	27	11	276

Colored photographs of frog species were used in each interview to identify those species that were collected, traded and consumed, respectively. To test the reliability of identifications, some species not occurring in the study areas were included. In general, the questionnaires included questions concerning the frog harvest (places and time, methods of harvest, species identities and numbers harvested), the economical and cultural importance of the frogs for the local population and the economic dimension (prices etc.). In most occasions, the interviewed persons were visited at home. The patriarchal society usually allowed solely talking with the family chiefs or with their sons. Accordingly, interviews with women were rare; market-women being an exception. Table 1 provides a summary of all interviews accomplished. These interviews were carried out between: January-March 2008 in Burkina Faso; March 2008 in Benin, and March-May 2008 and February-March 2009 in Nigeria. To evaluate the development of frog collection in Malanville an additional visit was undertaken in June 2009.

3.3 Results

3.3.1 Traded species

In Burkina Faso the African Tiger Frog, *Hoplobatrachus occipitalis,* was the most consumed species; followed by *Pyxicephalus edulis*, *Ptychadena bibroni*, *P. oxyrhynchus* and *P. trinodis* (Fig. 3.2). It was remarkable that toads, *Amietophrynus* spp.*,* also rank within the ten most consumed species. Toads seemed to be especially preferred by people in particular villages in Ganzourgou. In Nigeria, people likewise preferred *H. occipitalis* and all 23 interviewed traders traded them (100%), followed by *Xenopus muelleri* (26%) and *P. oxyrhynchus* (13%). *Xenopus muelleri* seem to be avoided by customers and traders in Burkina Faso. In general, large frogs were preferred over smaller ones. Consumers did not discriminate the sex of the consumed frogs; however, females tend to be larger. In Nigeria 44% of the collectors caught all frog sizes available in order to meet the demand.

3.3.2 Collecting seasons, sites and methods

Collection methods differed between villagers catching frogs for self-supply and commercial frog collectors. Within the latter group, 13 of the 22 interviewed persons stated to be fishermen. Eighty-two villagers in Burkina Faso provided details about collecting methods. They usually caught frogs in rivers or on the river banks (61%).

Many frogs, particularly *Hoplobatrachus occipitalis*, accumulate at rivers during the dry season (SPIELER 1997, RÖDEL 2000). Other collecting locations were temporary ponds (29%), dams (24%), wells (21%), permanent ponds (22%) and swamps (5%). Usually frogs got collected in close proximity (less than 1 km) to the collector's home (78%). In Nigeria the majority of frogs were caught from permanent ponds (81%; interviewees N= 32), followed by temporary ponds (72%), rivers (48%), swamps (32%), forests (16%), and wells (13%). Of all the 32 Nigerian collectors, 28% caught frogs all year round; 72% only collected frogs during the rainy season. The best time to catch frogs was during night and/or the early morning hours. In Burkina Faso the frogs got usually collected during the dry season (57%). Here the population mostly comprised farmers, which care about the cultivation of their fields during the rainy season and then do not have time to go after frogs. However, 29% of the villagers stated to collect frogs all year round and 13% collected them exclusively during the rainy season. All of the professional collectors (N= 22) caught frogs at rivers; 82% collected frogs during the dry season. Only one person (4%) caught frogs during the rainy season and three collectors (14%) caught frogs all year round.

In general, for villagers in Burkina Faso the consumption of frogs was more important than their selling. They (N= 82) usually caught frogs only by hand (79%). Some exceptions were

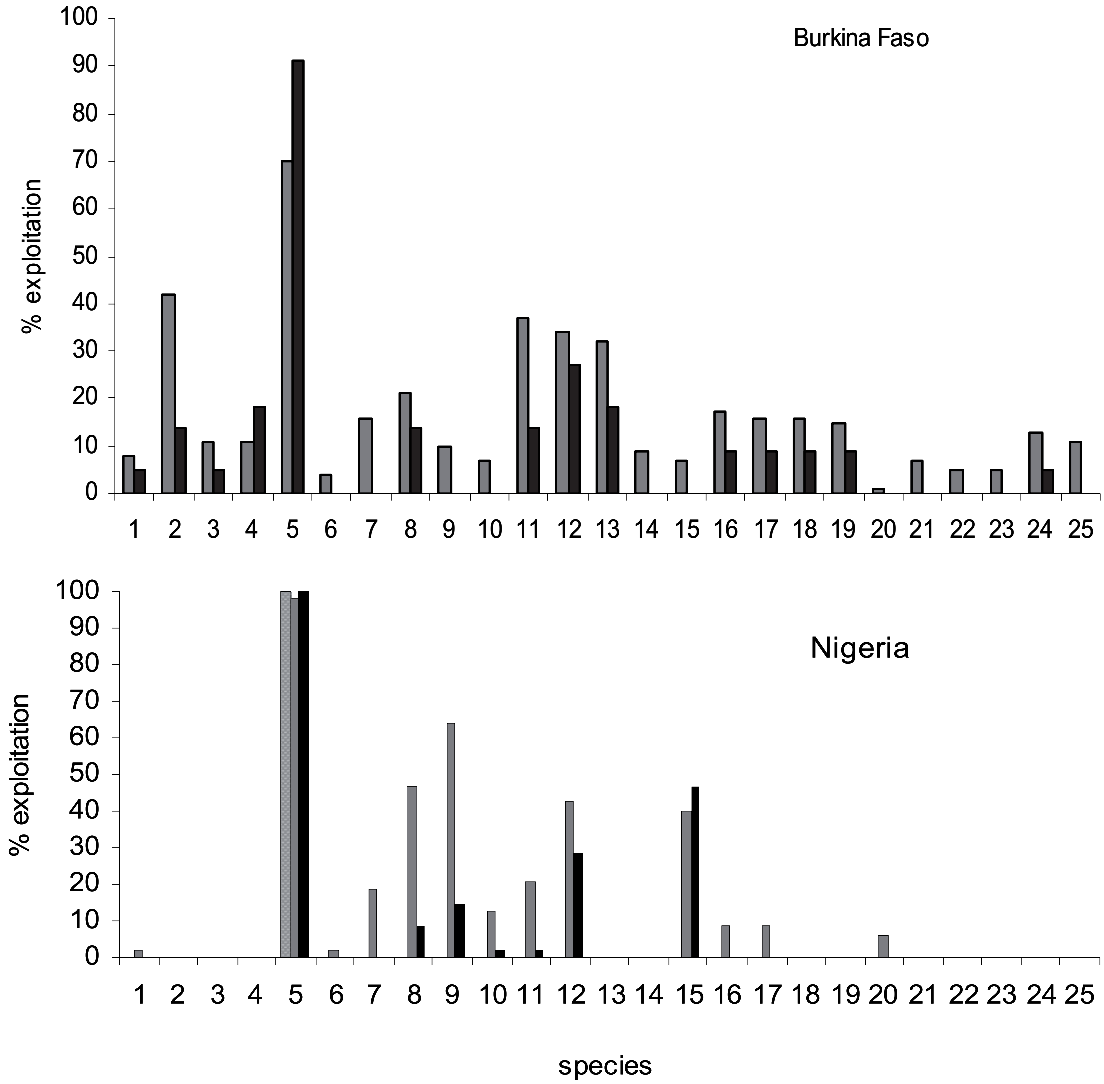


Figure 3.2. Species consumed and traded in Burkina Faso and in Nigeria, depending on how many times a species got pointed out on the photographs (consumed species: grey bars; traded species: black bars; species traded from Mallanville, Benin to Nigeria: grey patterned bar). Species listed by numbers: 1. *Hemisus marmoratus*, 2. *Pyxicephalus edulis*, 3. *Tomopterna cryptotis*, 4. *Hildebrandtia ornata*, 5. *Hoplobatrachus occipitalis*, 6. *Hylarana galamensis*, 7. *Ptychadena schillukorum*, 8. *P. pumilio*, 9. *P. mascareniensis*, 10. *P. tournieri*, 11. *P. bibroni*, 12. *P. oxyrhynchus*, 13. *P. trinodis*, 14. *P. tellinii*, 15. *Xenopus muelleri*, 16. *Amietophrnyus maculatus*, 17. *A. regularis*, 18. *B. pentoni*, 19. *A. xeros*, 20. *Hyperolius nitidulus*, 21. *Phrynobatrachus francisci*, 22. *P. natalensis*, 23. *Leptopelis viridis*, 24. *L. bufonides*, 25. *Kassina fusca*.

the use of hooks (23%), fishing nets (17%), dip nets (7%), basket traps (6%), truncheons (5%),chasing frogs out of small water puddles (5%), pitfalls (1%) and buckets which get quickly imposed on the frogs (1%). Thirty-two percent of the professional collectors caught frogs also with their hands. However, they tended to apply different catching methods. Fishermen often caught frogs in the same nets they use to catch fish (50%) or with hooks (23%). Further methods comprised: pit falls at the edge of dams (18%), basket traps (Fig. 3.3) which get placed in shallow water or swampy terrain over night (9%) or special dip nets (5%). In Nigeria frogs were caught with hands (80%) or with the help of fishing nets (75%)

followed by hooks (35%) and basket traps (25%). In 2008 all collectors in Malanville stated to use basket traps (N= 7). However, in 2009 the Nigerian frog collectors applied a different method. By the end of the dry season (June / July) they went out during night and used flash lights to detect the frogs by eye shine. With the help of long wooden sticks they beat the frogs on their heads. Given the high numbers of caught frogs (see below) this method seems to be the most efficient one.

Figure 3.3. *Hoplobatrachus occipitalis* caught with a basket trap in shallow parts of River Niger, northern Benin. The small fish are used as bait for the frogs.

In Burkina Faso collected frogs usually got sold to market-women, which first treat the frogs before selling them. Almost all frogs get fried in oil and then were sold one by one. Some market-women disembowel the frogs before they fry them; however frogs have been also fried and sold entire. In comparison, for the Nigerian market frogs were either smoked or dried.

3.3.3 Dimensions of frog trade

In Burkina Faso 80% of the 129 interviewed villagers stated that frogs are consumed in their villages. In Ganzourgou, 93% answered that frogs are consumed and 67% admitted that they eat frogs themselves. In Gourma 73% said that frogs are eaten and 48% told us that they themselves eat frogs. Twelve persons (9%) stated that they used to eat frogs in the past but stopped the consumption due to increasing prices or decreasing availability. Eighty-four villagers (65%) stated that frogs are an important food source for their families. Forty-three provided details concerning the amount of frogs they consume. Together, the 43 households (on average seven persons) consumed 262 kg of frogs per week; that is 6 kg (app. 120 frogs) per household per week. Often children, while herding cattle, collect frogs for their own consumption. Frogs thus seemed to be an important protein source for them. Of 54 interviewees 38 (70%) stated that they prefer to eat other meat like fish, beef, chicken, goat or sheep. Fifteen persons (28%) preferred frogs over other meat. Nearly one third of the villagers (29%) listed the frog trade as being a very important occupation. The majority of them depend on subsistence agriculture; however, 13 villagers (10%) stated that selling frogs was an important source of income during the dry season. In particular some collectors and market-women were dependent on the frog market.

The Burkina Faso frog economy was strictly partitioned between men and women. Whereas men were responsible for collecting, women were responsible for sale (Fig. 3.4). The only exception was the toad trade. Here, women are engaged in collecting, drying, and selling. Market women in Burkina Faso sold frogs mostly during the dry season. However, one fourth (25%; N= 24) traded frogs all year round. During the respective period many market-women (42%) sold frogs on a daily bases; one third (33%) sold frogs on 10 days per month. Twenty-two of 24 market-women stated that they altogether sell 65 920 frogs per months (app. 564 640 frogs annually). This included mainly Tiger Frogs and to a lower proportion toads. The price for one frog depended on its size and usually varied between FCFA25 for a small frog up to FCFA250 for a large one (exchange rate: EUR1.00= FCFA655.98).

Although the toad trade was locally restricted, it often comprised high numbers, e.g. one woman was meat processing 200 toads, all collected during one day. According to her she fills three sacks with toads per week, selling each sack for FCFA1500. Although the Burkina Faso frog trade is mainly a local one, market-women also receive orders from restaurants. In Ouagadougou most restaurants have frog legs on their menus; offering a plate for at least FCFA4000. In places like Mogtedo, located on main traffic axes, travellers often stop to buy larger numbers of fried frogs for their family and friends.

In Nigeria the frog trade had a different dimension. Frogs were mainly consumed in the South. In the states of the south-west a total of 32 frog collectors were interviewed. On average they collected 97 frogs per week (Fig. 3.5). Hence, these traders collected a total of 2780-3430 frogs per week, or 2 738 610 frogs annually (calculation including only periods where frogs are collected according to the interviewees). However, most traded frogs originated from the northern savanna zones in Nigeria, as well as from the neighbouring countries (Benin, Niger, and Chad). These frogs were transported to trading spots in northern Nigeria (e.g. Lollo, Kano, Benzu, Bagodo). At these places exclusive frog markets are

Figure 3.4. Woman selling dried toads on a market in a village in Ganzourgou, Burkina Faso.

organised. The traders in Lollo received their frogs mainly from Benin and Niger. Accurate numbers of harvested frogs could be obtained in Malanville, where frogs got collected exclusively for this Nigerian market. Many Malanville fishermen recently switched to the collection of frogs. On average a daily fish catch produced EUR2.00-3.00 income. Frogs were usually collected until at least one sack was filled (containing app. 1000 frogs). In 2008 that took about one week. One sack produced at least EUR15.00. Whereas the overall income thus was comparable, the advantage of selling frogs was receiving a higher amount of money once, thus providing more possibilities of spending the money. In contrast the daily income from fish often was spent straight away. In addition to the fishermen, Nigerian traders employed young Nigerians, who then travelled to and caught frogs in Malanville. In the latter case traders provided the trapping tools and picked the collected frogs once a week. In 2008 seven collectors filled on average 53 sacks of dried or smoked frogs per month. In 2009 the situation had changed drastically. An increased number of collectors, mainly coming from Nigeria, caught frogs. The authors accompanied a group of 30 collectors. On average a two-men-team caught 500 frogs per night (lowest numbers caught through full moon: app. 200-300 frogs per night and team; highest numbers: up to 1500 frogs per night and team). Based on the average numbers, these 30 collectors caught 450 000 frogs during their two-months-stay in Malanville. Either the collectors themselves travelled to Lollo to sell the frogs or traders purchased the frogs in Malanville and resold them in Lollo.

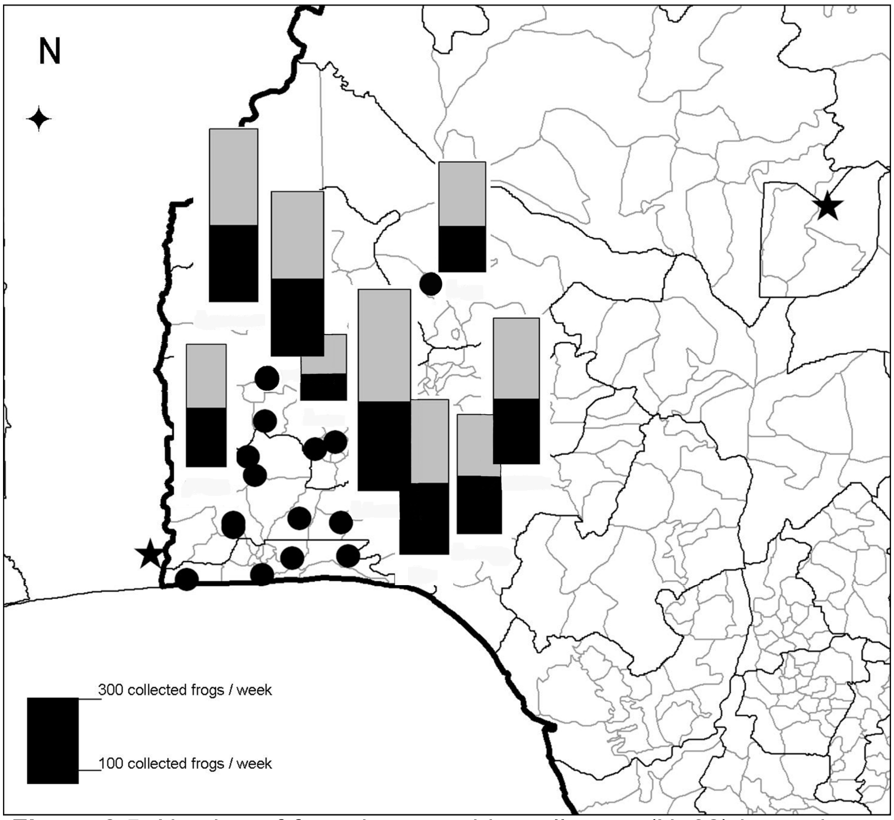


Figure 3.5. Number of frogs harvested by collectors (N=32) in southern Nigeria (black part: minimum average number of frogs collected per person per week; grey part maximum average number of frogs collected per person per week).

Usually a flat tax fee of FCFA1200 had to be paid when crossing the Nigerian border. Seventy to 80% of the frogs from the North were transported to Ibadan from where they got further distributed to other towns in Nigeria's southwest. In Ibadan frogs were also received from Chad all year round. These were collected at Lake Chad and passed through Maiduguri (capital of Borno State). From Kano (capital of Kono state) frogs were traded only during the rainy season. On average 5-10 frog sacks per trader got traded at one market-day in Lollo, e.g. five traders in Lollo traded 36-39 sacks per week (Fig. 3.6). Per sack they gain between Naira1000-2000 (NGN; exchange rate: EUR1.00= NGN196.70, a sack was NGN4000-6000 on purchase and NGN6000-10 000 on sale; Table 3.2). At subsequent trade centres, towards the South, the traded units got smaller. A frog-trade unit comprised 5-12 frogs (depending on their sizes) packed in bundles when being purchased and 3-7 frogs when being sold. A bundle was between NGN80-300 on purchase and generated NGN100-400 on sale (profit margin: 50-100%). Everywhere market prices depended on the size and quantum of frogs, but as well on the clients' negotiation abilities. According to 19 traders (83%) prices have been increasing over the past five years. The majority of traders traded frogs all year round, 22% traded them during the rain season only. Frog trade is predominantly for consumption, but some persons (13%) traded them also for medicine.

Figure 3.6. Frog market in Lollo, northern Nigeria. From here the frogs are transported into the South of the country.

Eighteen of 31 interviewed Nigerian customers bought frogs to consume them at home. Seven bought frogs to offer them in restaurants. In addition to the economic value of amphibians there was also a cultural value. Certain frog species have a medical importance, i.e. they are used to cure specific illnesses. Traditional medication is especially important in areas where western medicine is either not available or hardly affordable (VAN DER GEEST 1997). Especially toads and frog species looking similar to toads, as *Kassina fusca* and *Leptopelis bufonides*, were used in medical treatments.

Table 3.2. List of frog prices depending on the location and the stakeholder. Prices for Burkina Faso are in FCFA (exchange rate: EUR1.00=FCFA655.98, FCFA1000=EUR1.52). Prices for Nigeria are in Naira (NGN) (exchange rate: EUR1.00=NGN196.70; NGN1000=EUR5.08). For convenience, the prices in EUR are displayed in parenthesis. The frogs are listed in the (respective unit they get sold in (numbers of specimens, kg, bowls= 50-70 specimens, sacks= approximately 1000 specimens; box= >1000 specimens; (s)= small; (m)= medium; (l)= large).

Country	Location	Stakeholder	Purchase Unit	Price	(EUR)	Sale Unit	Price	(EUR)
Burkina Faso	Diabo	market-woman	3	100	(0.15)	1	50	(0.08)
	Diabo	market-woman	3-5	100	(0.15)	1	25-50-75-100	(0.04-0.08-0.11-0.15)
	Fada N'Gourma	market-woman	50 kg	10 000	(15.25)	1 (s)	50	(0.08)
	Fada N'Gourma, Mogtedo	market-woman				3 (s)	100	(0.15)
	Fada N'Gourma, Mogtedo	market-woman	1-3	50	(0.08)	1 (l)	100-150-250	(0.15-0.23-0.38)
	Zorgho	;market-woman	bowl	375	(0.57)	bowl	500	(0.76)
	Zorgho	market-woman	5 bowls	2500	(3.81)	4	25-50-100	(0.04-0.08-0.15)
	Zam	market-woman	2	50	(0.08)	1-3	100	(0.15)
	Kabouda	market-woman	bowl	565	(0.86)	8-10 (l)	50	(0.08)
	Kabouda	market-woman	bowl	500	(0.76)	8-10 (s)	25	(0.04)
	Kabouda	market-woman	bowl	500	(0.76)	Bowl	600	(0.92)
	Kabouda	market-woman	bowl	500	(0.76)			

Table 3.2. continued

Country	Location	Stakeholder	Purchase Unit	Price	(EUR)	Sale Unit	Price	(EUR)
Nigeria	Iseyin, Ilorin, Ogbomosho, Eruwa, Oyo Town, Epe, Ibadan	collector				5-6 (l)	100	(0.51)
	Ado-awaye, Abeokuta	collector				6-7 (l)	100	(0.51)
	Eruwa, Ado-awaye, Abeokuta	collector				12-15 (s)	100	(0.51)
	Iseyin, Ijebu Ode, Onidundun, Eruwa	collector				9-12 (s)	100	(0.51)
	Onidundun	collector				6-7 (m)	100	(0.51)
	Ijebu Ode, Iseyin, Eruwa, Ado-awaye, Abeokuta	collector				7-10 (m)	100	(0.51)
	Ijebu Ode	collector				6-8	100	(0.51)
	Epe	collector				8-9	100	(0.51)
	Iseyin	collector				sack(s)	500-600	(2.54-3.05)
	Iloron/Ogbomosho	collector				sack	700-800	(3.56-4.07)
	Ijebu Ode	collector				sack	200-800	(1.02-4.07)
	Odo Jabore	collector				sack	800	(4.07)
	Abeokuta	collector				sack	800-900	(4.07-4.58)
	Epe	collector				sack	1000	(5.08)

Table 3.2. continued

Country	Location	Stakeholder	Purchase Unit	Price	(EUR)	Sale Unit	Price	(EUR)
Nigeria	Lolo	trader	sack	4000-6000	(20.34-30.50)	sack	6000-10 000	(30.50-50.84)
	Iseyin	trader	bundle 6-10	150-200	(0.76-1.02)	bundle 3-5	80-90	(0.41-0.46)
	Iseyin	trader	bundle 5-10	150-200	(0.76-1.02)	bundle 5-10	250-400	(1.27-2.03)
	Ogbomosho	trader	bundle 6-7 (m)	80-100	(0.41-0.51)	bundle 8-10 (m)	100-200	(0.51-1.02)
	Ogbomosho	trader	bundle 5-6 (l)	150-200	(0.76-1.02)	bundle 3-4	100-150	(0.51-0.76)
	Ijebu Ode	trader	7-9 (m)	100-250	(0.51-1.27)	7-9 (m)	150-300	(0.76-1.53)
	Ijebu Ode	trader	5-6 (l)	100-250	(0.51-1.27)	bundle 5-6 (l)	150-300	(0.76-1.53)
	Oyo Town	trader	bundle 8-10	100-250	(0.51-1.27)	4-5	60-150	(0.31-0.76)
	Oyo Town	trader	9-12	80-250	(0.41-1.27)	4	50-100	(0.25-0.51)
	Oyo Town	trader	6-8	100-300	(0.51-1.53)	4	50-100	(0.25-0.51)
	Abeokuta	trader	8-12	100-300	(0.51-1.53)	8-12	150-350	(0.76-1.78)
	Pakoto(Ibo	trader	5-10	100-300	(0.51-1.53)	5-10	150-350	(0.76-1.78)
	Sagamu	trader	8-12	150-300	(0.76-1.53)	8-12	200-400	(1.02-2.03)
	Lolo	market-seller		6000-8000	(30.50-40.67)		6000-12 000	(3.05-61.01)
	Iseyin	market-seller	8-10	150-200	(0.76-1.02)	5-6	300	(1.53)
	Ibadan, Oyo Town	market-seller	box	12 000	(61.01)	6	100	(0.51)
	Ogbomosho	market-seller	box	10 000-13 000	(50.84-66.09)	5-7	100	(0.51)

Table 3.2. continued

Country	Location	Stakeholder	Purchase Unit	Price	(EUR)	Sale Unit	Price	(EUR)
Nigeria	Badagry	market-seller	40	1200-1400	(6.10-7.12)	6-7	200	(1.02)
	Epe	market-seller	50	1500-2000	(7.63-10.17)	4-5	150	(0.76)
	Abeokuta, Sagamu, Ijede	market-seller	5-6	100	(0.51)	8-12	200	(1.02)
	Oyo Town	market-seller	Box	9000-12 000	(45.76-61.01)	6	100	(0.51)

3.3.4 Declining frog populations?

Based on our informants' perception certain amphibian species have been declining during the past years. Most of the villagers (N= 129) thought that water shortage (46%) is the main reason for the frogs decline followed by consumption (15%), habitat degradation (7%) and population growth (5%). A different picture arose when asking fishermen (N= 22). They believed that the main reason for the amphibian species decline is habitat degradation (32%), followed by consumption and water shortage (both 23%). The villagers remarked highest decline rates in the largest species: *Pyxicephalus edulis* followed by *Hoplobatrachus occipitalis* and *Ptychadena oxyrhynchus*. According to our interviewees toads showed lowest decline rates. Some villagers even believed that toad numbers were increasing. When a decline was perceived, it was said that frog populations started to decline during the past two decades. These interviewees stated that reduced population numbers of particular frogs are the reason for their today's low presence on markets and that frogs were more consumed in the past. In northern Benin our interview partners at least partly observed declining frog populations. In Nigeria, only three of 32 persons perceived a decline of amphibian species; namely in *H. occipitalis*, *P. oxyrhynchus* and *Xenopus muelleri*, hence all three traded species. These three persons thought that the decline was due to over-hunting and habitat degradation. However, in Nigeria only the frog collectors were asked this question. Basically, in both countries the largest decline was perceived for the most exploited species.

3.4 Discussion

Recent investigations by WARKETIN et al. (2009) suggest an unsustainable exploitation of frogs in Asian countries. We herein report for the first time the local small-scale use of frogs in Burkina Faso and an intensive large-scale, cross-border frog trade between Nigeria and its neighbouring countries. Although the amount of traded frogs still is smaller than reported by WARKETIN et al. (2009), the West African amphibian collection, is likely to reach un-sustainability. Even during our, comparatively short observation time, we remarked a dramatic increase of frogs collected for the Nigerian food market. In Burkina Faso the frog use mostly was not a commercial one or restricted to a local scale. Whereas in Gourma most frog consumers caught frogs themselves, frogs were sold on markets in Fada N'Gourma and in the area of Diabo. For some species even this local consumption seemed to be unsustainable and interviewees in Burkina Faso indeed perceived a decline of frog populations, in particular of those species that were consumed. Indirect hints for an unsustainable frog harvest are especially the reports of increasing difficulties to catch frogs and increasing prices. Similar indications have been recently reported from western Cameroon and eastern Nigeria, where even tadpoles are collected for food (GONWOUO &

RÖDEL 2008). With my data I currently cannot judge whether the perception of declining frogs is real, and if so, if the decline would be exclusively due to overexploitation, or what effect other factors such as habitat degradation, pesticide use, climate changes (i.e. different rainfall patterns) etc. may have. Currently frogs can be harvested in all West African countries without any regulations, neither concerning time, species, numbers or sizes of harvested animals. Even more exploiters may enter the system as there is still a net return from the harvest. As there definitely is a huge social and commercial interest, frog collection and consumption being a very important part of villagers lives, it will be difficult to control or limit this frog harvest (LUDWIG 2001).

The methods used for collecting frogs varied by area and tradition, most of all however, with the intensity of the frog harvest. If frogs were used for self-supply only, catching them by hand was sufficient. In the areas with the most intense frog collecting activities, as in Malanville, basket traps seemed to a preferred and efficient method. Recently the Nigerian collectors switched to an even more effective method. They used torches to spotlight the frogs during night (KUSRINI 2005, TEIXEIRA et al. 2001), and then killed the frogs by beating their heads with long sticks. This method does not find application in Asia since damages would cause the rejection of the collected frogs, especially for those thought to serve the export (KUSRINI 2005).

The preference for frog species varied between places. The majority of customers and collectors preferred large specimens, but to meet the demand often all available sizes were collected. *Hoplobatrachus occipitalis* is a large and the main species used for food at all our study sites. *Ptychadena* spp. often got consumed but usually were not traded. *Xenopus muelleri* was the second most traded frog in Nigeria. Congeners of this species are also harvested for food in western Cameroon (GONWOUO & RÖDEL 2008). In contrast we did not get any hint that clawed frogs were eaten in Burkina Faso, although they are occurring here as well. Toads are only consumed in particular villages, e.g. in the Ganzourgou area in Burkina Faso, whereas in the neighbouring Gourma region nobody claimed to eat toads. Since large specimens are preferred for consumption the current rate of collecting may well lead to an altered population structure of *H. occipitalis*, or even result in local extinction. Unfortunately it is unknown at which age Tiger Frogs reaches sexual maturity. It is likely that frogs having reached about half of the maximum size (males 110 mm, females 160 mm; SPIELER 1997, RÖDEL 2000) already reproduce. Judging from similar sized frogs these could be about two years old. The largest adults may well be 10 years and older. An overexploitation of this species may not only have consequences for the long-term human alimentation but as well for the frogs' ecosystem. A loss of predators may weaken control of prey populations (ALLAN et al. 2005). In *H. occipitalis* this may apply to all life stages. This species has predatory larval stages preying on a variety of other aquatic animals, such as tadpoles and mosquito larvae, hence being an important element in the trophic cascade of temporary savanna ponds (SPIELER & LINSENMAIR 1997, RÖDEL 1998). Adult *H. occipitalis* feed on a variety of organisms, including potential pest insects (INGER & MARX 1961, LESCURE 1971). ABDULALI (1985) provides a detailed account on the ecology of some rice field dwelling amphibians in India (including another *Hoplobatrachus* species), highlighting their role as bio-control agents of rice insect pest control. Since India banned processing and export of frogs, the frog populations have recovered and insecticide imports have dropped by 40% (TEIXEIRA et al. 2001), indicating the large economic value of intact frog populations for pest control.

Ideally, any harvesting of wild species should be done sustainably (WAITES 2007). On a global scale an increasing number of internationally traded frogs are produced in frog farms (TEIXEIRA et al. 2001, DASZAK et al. 2006). Whereas there seem to be first efforts to set up frog farms in Central Africa (MUNYULI BIN 2002), I could not find any such initiative in West Africa. According to our data all West African amphibians used for food are from the wild. Although toads are consumed in some countries (DASZAK et al. 2006), ranoid frogs, and especially the American Bullfrog (*Lithobates catesbeianus*) and the Indian Tiger Frog (*Hoplobatrachus tigrinus*) are the most commonly bred species for consumption. The breeding of non-native species always bears the risk that a) specimens escape and harm native species and ecosystems (KIESECKER et al. 2001, BEEBEE & GRIFFITHS 2005) and b) import diseases (DASZAK et al. 2004). However, *H. occipitalis* is a species native in West Africa that might be possible to breed. There are first attempts of cultivating wildlife in northern Benin, especially concerning fish. It would be worthwhile trying to combine these efforts with breeding frogs.

A cultivation of *H. occipitalis* would not only help securing wild populations but also offering long-term socioeconomic advantages. The inland fishery sector can be indicative for the economical importance of the local frog trade. Besides the income that is gained from the fish catch, the processing of fish encompasses further economical benefits, i.e. employment. In other words, if fish can be produced and processed locally, the net income benefit to the area may be more than twice the value of the fish sales (FAO 2009). Similar advantageous may be expected by a captive breeding and processing program for frogs.

In West African countries small-scale fishers provide the majority of the national fish catch and contribute to about a quarter of the total protein in-take. Hence small scale fishing plays a vital role in nutrition, trade and economic activity (MARQUETTE et al. 2002). However, due to overexploitation in many inland waters fish stocks have drastically declined (ALLAN et al. 2005, BRASHARES et al. 2004). According to our data, amphibian collections rates increased in Malanville after fish populations in the Niger River declined. Similarly the harvest of wildlife increased in Ghana following declining fish stocks. There years of poor fish supply coincides with increased hunting rates and thus resulted in the decline in biomass of wildlife (BRASHARES et al. 2004). The increasing West African demand for frogs thus may be an indirect sign for an alarming decrease of other natural resources and deserves more attention.

Although most decision-makers in West African countries are well aware of the need for wildlife conservation, they are mostly confronted with more pressing problems, such as health, education, food and agriculture. Having limited funding available; wildlife conservation usually has low priority (NTIAMOA-BAIDU 1987). However, the dimension of frogs currently traded in parts of West Africa may be not only a sign for further problems in nature conservation. The decline or even potential loss of frogs in particular areas may have direct and indirect effects on rural communities, such as potentially increasing mosquito populations, less bio-control of agricultural pest species or negative effects on freshwater ecosystems such as temporary ponds (MOHNEKE & RÖDEL 2009). To address these question in more depth, more basic data on the quantity of traded frogs, their origin and their customers, as well as basic data on natural frog abundances, population structure, and life history data for modelling approaches (i.e. to develop management programs for sustainable harvests) and breeding programs are urgently needed.

4 Amphibians as food and medicine in West Africa

4.1 Introduction

Since pre-historic times, wildlife has been exploited by humans (LEAKEY 1981, KYSELÝ 2008). Being an essential protein source, animals have been hunted, fished or collected in all human societies. In rural Africa local people still predominantly depend on the natural resources provided by the environment they inhabit. Numerous ethnobiological surveys have investigated the dependence on wildlife in Africa (e.g. ADEOLA 1992, BALAKRISHNAN & NDHLOVU 1992, OSEMEOBO 1992). These authors mainly detected the hunting and use of mammals, birds and reptiles. In addition to their use as food, these animals often likewise play an important role as medicine, in traditional beliefs, or simply as a source of income (AKPONA et al. 2008). For example in the Lama forest area of southern Benin, rodents and three-cusped pangolins are hunted for food, but as well as a source of income (ASSOGBADJO et al. 2005, AKPONA et al. 2008). In Gabon the water snake *Grayia ornata*, is regarded as an excellent food by locals, however, it is also used as a medicine and in magical rites (PAUWELS et al. 2002).

In contrast to the above mentioned animal groups, there is comparatively little information available about the use of amphibians in Africa, although they are used globally (TEIXEIRA et al. 2001, KUSRINI & ALFORD 2006, MOHNEKE et al. 2009, WARKENTIN et al. 2009). In addition to their value as food, amphibians are used for medicinal and cultural purposes (e.g. as totem, fetish or in particular ceremonies) as well as in other day to day activities. For instance South American Indians use the skin secretion of poison arrow frogs of the family Dendrobatidae for hunting (MYERS et al. 1978, LÖTTERS et al. 2007). In north-eastern Australia frogs find applications in the culture and mythology of the Aborigines (BOLL 2004), based mainly on the perceived affiliation between water and frogs. The frog, called Garkman, symbolizes the wet season and the weather in general.

In Africa, amphibians have probably always been used as food and for cultural purposes; however, detailed information about both aspects of use is rare. A study by PAUWELS et al. (2003) reported the cultural use of amphibian species by two ethnic groups (Massango Bantu and Babongo Pygmies) in Gabon. In particular these authors documented how the treefrog *Leptopelis notatus* is incorporated in traditional beliefs and mystical use, and how the traditional belief (use in ethnic wars) was adopted to modern lifestyle (soccer). GONWOUO & RÖDEL (2008) investigated the use and cultural significance of various amphibian species in the Mount Manengouba area in western Cameroon. In Madagascar JENKINS et al. (2009) observed a harvest of edible, endemic frog species (*Mantidactylus* spp.) as culinary offers in restaurants. With regard to the world wide amphibian decline (STUART et al. 2008) recording such ethnozoological data is important since traditions likely will disappear when a given ethnic group is no longer in contact with a particular species because of its extinction (PAUWELS et al. 2003).

In the scope of unrevealing the amount and means of traded frogs within and between West African countries (Burkina Faso, Benin and Nigeria, see chapter 2), I simultaneously collected ethnozoological data about the use and traditional significance of various West African frog and toad species. I herein report these findings with special reference to the use of amphibians by specific ethnic groups (Mossi, Gourmanché, Yoruba, and Hausa), in different countries (Burkina Faso, Nigeria) and with regard to religion (traditional beliefs, Christianity and Islam).

4.2 Methods

The study was conducted in Burkina Faso and Nigeria, West Africa. Our main focus in Burkina Faso was on two regions: the province of Gourma in the southeast, and the province of Ganzourgou in the centre of the country. For a detailed map of the villages see Fig. 3.1). The Mossi (language: Mooré) are the dominant ethnic group in Ganzourgou. They have maintained much of their traditional society's structure (KONSEIGA 2005) and are primarily farmers. In contrast the province Gourma is the home of the Gourmanché (language: Gulmancéma). However, many Mossi moved into the latter region and the majority of the villages in Gourma now comprise quarters where the Gourmanché and the Mossi live, respectively. In comparison to the rest of the country, Gourma is poorer and less developed.

In Nigeria, our main focus was onto frog trading spots in the state of Kebbi, in the northwest and the larger cities and towns in the southwest of the country (states of Ogun, Oyo, and Lagos). Nigeria has the highest human population on the African continent, comprising about 250 ethnic groups. In our study areas the dominant ethnic groups are the Hausa and Yoruba. The latter live mainly in the southwest of Nigeria, but also in other parts of Nigeria, Benin, Ghana and Togo. In Nigeria they account for 21% of the population. The Hausa are likewise an ethnic group with a very wide distribution. Hausa groups live all over the savanna zone of West and Central Africa, but particularly they have settled in the North of Nigeria.

Semi-quantitative structured questionnaires, as described in chapter 3, were used to investigate the frog trade in Burkina Faso, Benin and Nigeria. Ethnozoological questions addressed the identity of used species, the mode of collecting them, the particular use of amphibians (food, medicine, mythic subject), as well as the economic and cultural importance of these frogs for the local human population. Colour photographs of frog species were used in each interview to identify the respective species. The study was undertaken in the dry season because during the rainy season villagers are usually occupied with cultivation and stay on their fields. Between January and March 2008 a total of 175 interviews were accomplished in Burkina Faso: 129 with family chiefs, 24 with market-women and 22 with fishermen. In Nigeria (total number of interviews: 112), 32 interviews were carried out with frog collectors, 23 with traders, 26 with market-sellers, and 31 with customers.

4.3 Results

4.3.1 Methods of collecting frogs

In my study areas amphibians were caught in many different ways. However, only one fourth of the interviewees in Burkina Faso reported how they catch frogs. Most frequently the villagers searched frogs actively and caught them by hands. In contrast fishermen mainly caught frogs with their fishing nets, both deliberately and as by-catch. In swampy areas with shallow water, basket-traps were a more efficient method. These traps were usually placed in the water in the evening. Small fishes were added as bait for the frogs (mainly *Hoplobatrachus occipitalis*). One fisherman developed a very large basket-trap, being more than 1 m high and long (Fig. 4.1). With this trap he could collect up to 400 frogs per night. This successful invention has fast been adopted by others and is now used by most fishermen in the respective village in Burkina Faso. In 2009 I observed an even more efficient method used by Nigerian frog collectors in Malanville, Benin. These collectors used torches to blind the frogs at night and then beat the frogs to death with long wooden sticks (mean number of frogs collected per night and team = 2 persons: 500 frogs; see Chapter 3). I also observed that frogs may be caught with fishing hooks, too. However, the number of frogs collected with the latter method was few. Further sporadic catching methods were e.g. a pair of handmade dip-nets (Fig. 4.2), which can be very successfully applied in smaller puddles, or a bundle of long dried grass, being wiped by 3 or 4 persons through a shallow pond. The frogs are thus chased out of the water and subsequently collected. One observed method, often applied by fishermen, was the creation of troughs next to water bodies such as dams (Fig. 4.3). The troughs were covered with vegetation to create an attractive cool and shaded shelter for frogs. When they exit the water during night they would frequent the trough until the collector harvests them the next day.

Figure 4.1. Basket trap exclusively designed for catching frogs. Up to 400 frogs can be caught with this trap within one night; seen in a village in Ganzourghou, Burkina Faso.

Figure 4.2. Traditional dip-net used to catch frogs in smaller puddles and ponds. The picture was taken in Gourma, Burkina Faso.

Figure 4.3. Trough covered with vegetation to attract and catch frogs over night.

4.3.2 Different species – different values

Based on our interviews, at least 37 different frog and toad species were consumed in Burkina Faso, compared to 14 species in western Nigeria. In Burkina Faso the majority of the amphibian fauna was familiar to the interviewees and most species have names in the local languages (Mooré and Gulmancéma, Tab. 4.1). The species which has been most often cited as being used and which has been collected in largest quantities was the African Tiger Frog, *Hoplobatrachus occipitalis*. In all study regions it was the primary frog species traded and used for consumption. The various ways of its preparation are explained below. The Edible Frog, *Pyxicephalus edulis*, is another large species preferred for consumption, 41% of the interviewees (N= 129) stated to consume/catch this frog. However, this species is hard to find as it lives buried in the ground for most of the year (RÖDEL 2000).

In addition to its meat, people use the skin of this frog, which is very resilient, to fabricate drums. In particular, children's drums are crafted of this frog's skin. The genus *Ptychadena* comprises medium sized to larger frog species with especially long, muscular hind legs (RÖDEL 2000). When knowing where to search for them, it is comparatively easy to catch them during the dry season. At that time they usually hide beneath stones or in cracks in humid soil. However, the collecting effort is much higher than for the African Tiger Frog and people thus tend to retain *Ptychadena* spp. for their own consumption, instead of selling them on markets.

Table 4.1. List of West African frog species occurring in the study areas in Burkina Faso. Given are scientific, English and local names and the frog species' principal way of being locally used (Cs= consumption; Cl= cultural use; M= medical use, see Tab. 4.2); *based on RÖDEL (2000) and FROST (2009).

Scientific name	English*	Mooré	Gulmancéma	Usage
Afrixalus vittiger	Spiny Reed Frog	Poond youga	Tiarli moanga	
A. weidholzi	Weidholz's Banana Frog	Poond youga	Pouang piéga	
Amietophrynus maculatus	Hallowell's Toad	Poond sablga	Pouand boani	Cs, M
A. regularis	Egyptian Toad	Poond sablga	Pouand koulougou	Cs, M
A. xeros	Desert Toad	Poond miougou	Pouand gnouali	Cs, M
Bufo pentoni	Shaata Gardens Toad	Kossoilhg poondré	Gnissolopouandi	Cs, M
Hemisus marmoratus	Shovel-nosed frog	Yoondé	Pouandi napoualé	Cs
Hildebrandtia ornata	Budgett's Burrowing Frog	Souansga	Tiarlo	Cs
Hoplobatrachus occipitalis	African tiger frog	Louanga	Louandi moali	Cs
Hylarana galamensis	Yellow-striped Frog	Boulwéoogo	Tiarli pieno	Cs
Hyperolius concolor	Hallowell's Sedge Frog	Pouand youga	Pouand piéga	
H. nitidulus		Pouand youga	Tiarli moanga	Cs
Kassina cassinoides		Poondr zembouanga	Tiarli bouanga	
K. fusca	Pale Running Frog	Poond bougdi	Pouand bouanli	Cs, M
K. senegalensis	Senegal Kassin's Frog	Poondr zembouanga	Tiarli bouanga	
Leptopelis bufonides	Ground Tree Frog	Poond sablga	Pouand koulougou	Cs, M
L. viridis	Savannah Tree Frog	Poond youga	Gnissolopoanga	Cs
Phrynobatrachus calcaratus	Boutry River Frog	Louang sablga	Patanpouandi	
P. francisci		Louong sablga	Pouand bouanga	Cs
P. gutturosus	Guttural Puddle Frog	Boulwéoogo	Pouand bouanga	
P. latifrons	Accra River Frog	Boulonboukou	Batiarlo	
P. natalensis	Natal River Frog	Boulghin louanga	Thialondo	Cs
Phrynomantis microps	Red Rubber Frog	Poond wiilé	Pouang moanga	

Table 4.1. continued

Scientific name	English*	Mooré	Gulmancéma	Usage
Ptychadena bibroni	Broad-banded Grass Frog	Mouonghin souansga	Foipoando	Cs
P. mascareniensis	Mascarene Grassland Frog	Bouonghin souansga	Tiarli Bouanga	Cs
P. oxyrhynchus	Sharp-nosed Rocket Frog	Biihrin souanga	Pouand pièga	Cs
P. pumilio	Little Rocket Frog	Poughin souansga	Tiarli moanga	Cs
P. schillukorum	Schilluk Ridged Frog	Louang sablga	Pouandi gnoanli	Cs
P. tellinii	Central Grassland Frog	Tampou souansga	Tiarli gnoiarlinga	Cs
P. tournieri	Tournier's Rocket Frog	Biihrin souansga	Tiarli gnoanrga	Cs
P. trinodis	Dakar Grassland Frog	Boulonboukou	Pouand gourou	Cs
Pyxicephalus edulis	Edible Frog	Boulonboukou	Pouandi koulougou	Cs, Cl
Tomopterna cryptotis	Cryptic sand frog	Poondré	Pouandi bouali	Cs
Xenopus muelleri	Savanna Clawed Frog	Louang boudi	Louand boani	Cs

The Clawed frog, *Xenopus muelleri*, was usually not collected and consumed by people in Burkina Faso. In contrast in Nigeria, this species was one of the three most often consumed and traded species. Similar observations have been reported from western Cameroon (GONWOUO & RÖDEL 2008). *Xenopus.muelleri* inhabits the banks of tributaries of larger rivers during the dry season and move into the savanna during rainy season, where it colonizes and breeds in savanna ponds. It also accumulates in open permanent and well like waters and thus is a species easy to harvest all year round (Rödel 2000).

In comparison to other frogs, toads are easy to catch. They often accumulate and hide under stones, branches, leaves etc. during the dry season and usually occur in large numbers close to and even within villages. In particular areas in Burkina Faso toads are collected all year round, mainly to be sold on local markets (Fig. 4.5). Because of their warty skin other frog species, like *Kassina fusca* or *Leptopelis bufonides,* are sometimes taken for toads (19% of interviews, N= 129).

Besides their use as food items, they are applied in medical treatments to cure specific illnesses (see below). Species, which were only rarely mentioned to be used, are small tree and leaf-litter frogs of the genera *Afrixalus*, *Hyperolius*, *Leptopelis* and *Phrynobatrachus*. But even these frogs may have some meaning to local people, e.g. we were told by an old Mossi patriarch in Gourma that pregnant women should avoid touching a *Hyperolius*. If by bad luck such a frog jumps on a pregnant woman or the woman touches the frog, her child will become very weak and will always be sick.

4.3.3 Frog meals

There are various ways of processing and preparing frogs in West Africa. However, with the exception of frogs offered in more expensive hotels and restaurants, frogs are usually consumed in one piece. Mostly the intestines are removed and sometimes head and feet are cut off as well. The way of preparation depends on the circumstances where and when the frogs get consumed, i.e. at home, on the market, in restaurants, immediately, later on etc. Altogether we came across the following ways of preparation in Burkina Faso (answers of 129 interviewees): smoked (35%), cooked in a soup (29%), prepared in sauce and served with rice (26%), grilled (24%), dried (17%), fried (12%), and cooked (2%).

Children sometimes catch frogs and grill them on a fire while they are herding the cattle (Fig. 4.4). If they bring them back home the women prepare the frogs in a soup or in a sauce which is usually served with rice.

Figure 4.4. Children roasting frogs over a fire in Gourma, Burkina Faso.

Figure 4.5. Toad trade in Ganzourghou, Burkina Faso. Every third day women from various villages meet at the market in Zorgho to trade dried toads.

Figure 4.6. Frogs getting sun-dried in Malanville, Benin.

On the markets in Burkina Faso frogs were always offered deep-fried. Prior to deep-frying frogs sometimes are partly sun-dried or coated with flour. On local markets people either buy fried frogs as snacks and eat them with salt and chilli or take them home to prepare a soup. For toads we recorded only one way of preparation. Most of the interviewed women, trading toads in Burkina Faso (78%, N= 9), stated that the toads are sold dried (two women did not answer to this question). These dried toads then were added to meals (e.g. in a sauce) or were eaten as a snack (Fig. 4.5).
Frogs caught in the savanna region for the southern Nigerian markets have to be transported over long distances, sometimes even across country boarders. Since durability is thus important, frogs collected for this market got either sun-dried or smoked soon after being collected (Fig. 4.6). These procedures seem to assure that the frogs are preserved for quite some time without starting to rot.

4.3.4 Frogs as medicine

In total we recorded 14 different amphibian species being used as medicine in Burkina Faso. Of all people interviewed in Burkina Faso (N= 129) 64% used frogs to cure diseases, one person used frogs as fetish and for 34% of the persons frogs had no cultural meaning at all. The following species got used by those interviewees knowing frogs and toads as medicine (N= 82, most interviewees mentioned more than one species): *Bufo pentoni* (77%), *Amietophrynus regularis* (54%), *A. maculatus* (53%), *A. xeros* (43%), unidentified toads (58%), *Kassina fusca* (10%), *Tomopterna cryptotis* (6%), and *Leptopelis bufonides* (6%). The last three frog species (Families: Hyperoliidae, Pyxicephalidae, Arthroleptidae, respectively) had been classified as toads (Family: Bufonidae) by the interviewees ("toad" like appearances) and are usually used for the same diseases and via the same modes of application (Tab. 4.2).
The diseases which we recorded to be cured with amphibians were cough (40%), particularly in children; followed by appendicitis (21%), wounds (5%), measles (5%), scorpions stings (5%), furuncles (4%), face pain (4%) and others (4%; including: pruritis (itchy scratch), enuresis (bed wetting), umbilical hernia, and lack of appetite in children, Tab. 4.2). Since there has been a very high frequency of acute respiratory infections among children in Burkina Faso (LANG et al. 1986) this might be one reason why it is the most frequent complex of diseases to be treated. The mortality rates related to acute respiratory infections in Burkina Faso are among the highest in the world. It is estimated that these diseases are responsible for 20 to 40% of the total death rates among children below five years of age!
To cure cough the toads get prepared in a soup. The same application was used to cure measles. In case of an acute appendicitis the skin of the right side of the patient's abdomen

Table 4.2. Diseases healed by using West African amphibian species and the respective treatment of these species.

Disease	Amphibian species used in healing	Treatment
Cough	*Amietophrynus maculatus, A. regularis, A. xeros, Bufo pentoni*	animals get skinned and prepared in a soup
Appendicitis	*Hoplobatrachus occipitalis, Pyxicephalus edulis, Tomopterna cryptotis*	Skin of right belly carved (usually with a razorblade), frogs is rubbed over the scratches
Wounds	*A maculatus, A. regularis, A. xeros, B. pentoni, Kassina fusca, Leptopelis bufonides, T cryptotis*	Inner surface of frogs' skin attached on wound and left for several days (up to 10 days)
Measles	*A. maculatus, A. regularis, A. xeros, B. pentoni, K. fusca, L. bufonides*	Frog cooked in soup
Furuncle	*A. maculatus, A. regularis, A. xeros, B. pentoni, T. cryptotis*	Frog cooked in soup
Face ache	*A. maculatus, B. pentoni, L. bufonides*	Skin on temples carved (usually with a razor blade), frog rubbed over scratches
Scorpions' sting	*A. maculatus, A. regularis, A. xeros, B. pentoni, T. cryptotis*	Animal are either rubbed over sting location or attached at this spot and left there for several hours (the toad dies during this procedure)
Bed-wetter	*Ptychadena oxyrhynchus, P. trinodis*	Frogs get fried and mixed with other ingredients; oral application
Umbilical hernia	*A. maculatus, A. regularis, A. xeros, B. pentoni, P. edulis, T. cryptotis*	Carving patient's skin and rubbing toad on scratches
Diverse: itchy scratch, loss of appetite in children	*A. maculatus, A. regularis, A. xeros, B. pentoni, P. edulis, P. oxyrhynchus, P. trinodis, T. cryptotis*	First: rubbed over or attached to itchy scratch. Latter: frog cooked in soup

got scratched with a razor blade until the scratches started bleeding. Then a living toad was rubbed over the wound. The same method was applied when having facial pain, but here the temples got scratched and rubbed over with a toad. When curing open wounds, scorpion stings or furuncles the toads got first skinned. Then the skin was tied onto the wounded spot with the outer toad skin layer being in contact with the affected area. The toad's skin remained for the time until the wound was healed. It is notable that there were differences between ethnic groups in using amphibians in traditional medicine. Gourmanché were curing cough with the help of toads more often (73%, N= 33) than Mossi (23%). In contrast, curing

appendicitis with toads was more often applied by Mossi (71%, N= 17) than by Gourmanché (29%). Respective differences were recorded for other diseases like for measles, facial pain or scorpion stings. Generally we observed that curing with frogs was more often applied by Gourmanché (85%, N= 47) than by Mossi (51%, N= 82, X^2 test, χ^2= 9.391, df = 1, p= 0.002).
Differences in the use of amphibians in medicine was not only observed between ethnic groups, but was mirrored by comparing different study regions in Burkina Faso. Ninety percent of the interviewees (N= 82) using frogs as medicine were living in Gourma (dominated by Gourmanché) and only 10% were from Ganzourgou (X^2 test, χ^2= 64, df = 1, p< 0.001). In Gourma alone, 85% of the Mossi (N= 40) used frogs for curing. We did not gather information about frogs as medicine in Nigeria. Some authors like ADEOLA (1992) have shown the importance of wildlife for cultural and medical purposes in Nigeria. This author did not mention the use of amphibians; however, one of our Nigerian informants, who described himself as a traditional healer, said he would buy toads on the markets for healing purposes only.

4.3.5 Who is collecting, trading and eating frogs?

With regard to customs in consuming frogs I interviewed people from different regions, ethnic groups, and religions (Tab. 4.3). In Burkina Faso we detected signs of potential regional differences. There was a –non significant– trend for a higher rate of frog consumption in Ganzourghou compared to Gourma (X^2 test, χ^2= 3.139, df = 1, p= 0.076). However, using frogs as food was similarly common between Mossi (59%, N= 82) and Gourmanché (47%, N= 47, X^2 test, χ^2= 1.359, df= 1, p= 0.244).
Likewise I did not record significant differences in frog consumption customs between interviewees of different religions (X^2 test, χ^2= 1.321, df= 2, p= 0.517). When Gourmanché denied the practice of eating frogs, this was explained by the fact that their parents did not consume these either, demonstrating the importance of family traditions in Africa.
I did not detect any gender related differences in frog consumption. However, there were gender differences concerning the frog catch and trade. In Burkina Faso, fishermen were mainly responsible for the catch and women took care of preparation and selling. This way both, husband and wife were sometimes involved in the frog trade. Hence both depended on the income gained through frogs. As people often not temped to make large differences between amphibians and fish, these got treated together: fishermen caught both animal groups and market women usually sold them together. We observed an exclusive market of toads in Zorgho in Ganzourghou (Fig. 4.5). In this trade only women are involved, being self-organised in collecting and trading.

Table 4.3. Percentages (and absolute numbers in brackets) of the different respondents (N= 129) according to origin (two regions in Burkina Faso), ethnic identity and religion.

	Location		**Ethnic identity**		**Religion**		
	Gourma	Ganzourgou	Gourmanché	Mossi	Moslem	Christ	Animist
Interviewees	67% (86)	33% (43)	36% (47)	64% (82)	40% (51)	47% (61)	12% (15)
Interviewees from villages where frogs are consumed	73% (63)	93% (40)	68% (32)	87% (71)	82% (42)	80% (49)	80% (12)
Interviewees claiming to eat frogs	48% (41)	67% (29)	47% (22)	59% (48)	49% (25)	59% (36)	60% (9)

The interviews, that were conducted in Nigeria included primarily the ethnic groups Yoruba and Hausa (Tab. 4.4). Concerning customers, all Hausa claimed not to consume frogs. On the other hand 68% of the interviewed Yoruba stated to consume frogs. Although the frog trade was mainly in Yoruba hands as well, Hausa were also actively collecting and trading frogs in the North. Some important frog trading points like Kano were controlled by Hausa.

Table 4.4. Percentages of interviewees belonging to different stakeholder groups involved in the frog market, according to ethnic identity, religion and gender (in brackets the number of responding persons is provided).

Ethnic group / religion / gender	**Nigerian collectors** (N= 32)	**Benin collectors** (N= 7)	**Traders** (N= 23)	**Salespersons** (N= 26)	**Customers** (N= 31)
Hausa	0% (0)	100% (7)	39% (9)	31% (8)	16% (5)
Yoruba	91% (29)	0% (0)	52% (12)	65% (17)	81% (25)
Others	9% (3)	0% (0)	9% (2)	4% (1)	3% (1)
Moslems	16% (5)	100% (7)	44% (10)	39% (10)	23% (7)
Christians	84% (27)	0% (0)	57% (13)	58% (15)	71% (22)
Women	28% (9)	100% (7)	22% (5)	50% (13)	26% (8)
Men	72% (23)	0% (0)	78% (18)	50% (13)	74% (23)

4.4 Discussion

My study data reported herein and in chapter 3, revealed the importance of frogs as food and medicine, as well as a source of income for various West African people. The use of frogs as food definitely is of large economic importance as has been outlined elsewhere. However, whereas the local trading and consumption of frogs and their use as medicine have

assumingly long been part of the respective cultures, our observations point into the direction that a regional and cross-border frog trade has evolved only recently (MOHNEKE et al. 2010).
The inclusion of various levels of participants in the trade, offers a broad range of income sources. Positive in this respect is also the participation of women. The broad range of different methods for catching frogs, the different ways of preparation and last but not least the large-scale geographical range of the frog use, are signs for a long lasting tradition of frog use in West Africa. According to AUERBACH (1995), amphibians do not play an important part in most African cultures. He estimates that only 20% of local amphibian faunas are known and named by local people. My results did not support this assumption and the range of local names for amphibian species might be a sign for their meaning in West African culture.
One part of this culture is traditional healing. Whilst “western” medical treatments are becoming commonplace, traditional medications are still of huge importance in many rural, poor and remote places. Here people still rely heavily on plant and animal based traditional medicine products (NTIAMOA-BAIDU 1987). I cannot judge whether the various treatments of diseases with frogs and toads are effective. In this respect it remains questionable if the preparation of toads in soup is an effective treatment since the heat may inactivate many or all of the potential toxins and beneficial compounds found in toad skin glands. On the other hand, treatments that incorporate the direct contact of toad skin to infected areas and wounds could benefit from antibacterial actions of specific skin components. In any case, to many people in the investigated villages frogs certainly are of importance. In fact using frogs in medicine is known globally. For instance some native North Americans, Huron and Iroquois, used dried wood frogs (*Rana sylvatica*) as medicine (in THOMAS 1996). In British folk medicine, toads got used as a treatment against cough, warts and inflammations of the skin (HATFIELD 2004). Toads have been used in China as a heart medicine and against dropsy and it was even tried to use them to combat the plague in the Middle Age (HATFIELD 2004). Other animals are likewise used in traditional medicine, e.g. in Brazil respiratory diseases are cured by using particular fish species (COSTA-NETO 1999, BEGOSSI et al. 2006).
Skin toxins naturally protect frogs and toads from fungi and bacteria, and in some more venomous species, from being swallowed by other animals. The medical activity of various skin components has been confirmed by modern pharmacology as having high potential in either ultimately being of help in curing various diseases or at least being the basis for derivates and respective drugs against cancer, as pain killer, or even to prevent cells from being invaded by HIV (e.g. CLARKE 1997, DALY 2003, VAN COMPERNOLLE et al. 2005, PUKALA et al. 2006, GARG et al. 2008, LU et al. 2008). The local use of particular frogs and toads in traditional medicine has the potential to hint on promising substances for future drugs. As long as rural people cannot afford conventional medicine, the respective natural resources

have to be harvested in a sustainable manner in order to maintain access to them. It is therefore worrying that, during the last 10 years, the West African frog trade seems to have constantly increased in various regions in Burkina Faso and Nigeria, potentially to unsustainable levels. One reason for that might be the decline of other natural resources, such as fish (MOHNEKE et al. 2010). However, a sustainable use of amphibians in this region is not only important with regard to a durable source of proteins and medication, the frog and toad species in question offer also a variety of ecosystem services being of not less importance to the rural population (MOHNEKE & RÖDEL 2009). Maintaining a healthy community of frog species is thus essential for the ecosystem, as well as for humans with respect to their nutritional and medical needs.

5 Tadpole communities of ephemeral savanna ponds in different disturbance regimes in Burkina Faso, West Africa

5.1 Introduction

Amphibians are affected by a worldwide decline with possibly dramatic consequences on entire ecosystems. Reasons for their decline are numerous, and comprise among others habitat destruction, climate change, invasive species, disease, and overexploitation (GIBBONS et al. 2000, HOULAHAN et al. 2000). In West African savanna regions, habitat degradation is mainly generated due to an increasing human population followed by intensified agriculture and livestock herding. Those disturbed habitat regimes may affect species richness and furthermore the composition of amphibian communities (e.g. PEARMAN 1997, LEHTINEN et al. 1999, ERNST & RÖDEL 2008, HILLERS et al. 2008). Anthropogenic activities often lead to altered environmental conditions, which are not suitable anymore for certain species and subsequently result in altered species assemblages. Former studies, which have investigated alterations of amphibian assemblages due to anthropogenic disturbances mainly focused on adult communities in tropical forest habitats (e.g. ERNST & RÖDEL 2005, 2008, HILLERS et al. 2008). In this study we concentrate on freshwater savanna ecosystems and their tadpole communities.

Besides altered habitat factors due to human activity, in particular overexploitation could additionally affect community compositions in disturbed regimes (MORA et al. 2007). In the past decade the research interest concerning the consequences of the overexploitation of amphibian species increased considerably (TEIXEIRA et al. 2001, SCHLAEPFER et al. 2005, KUSRINI & ALFORD 2006, CARPENTER et al. 2007, WARKETIN et al. 2009). We recently reported a trend towards overexploitation of the West African tiger frog (*Hoplobatrachus occipitalis*) in West Africa (MOHNEKE et al. 2010). Exploitation usually concerns a number of specific amphibians. In West Africa this concerns especially species which are large enough to serve as food including African tiger frogs (*H. occipitalis*), African bullfrogs (*Pyxicephalus edulis*) and various *Ptychadena* species. In cases of unsustainable exploitations, the respective species are declining and may eventually become locally extinct (TEIXEIRA et al. 2001, TYLER et al. 2007, WARKETIN et al. 2009). Concerning *H. occipitalis*, overexploitation probably continues until harvest is not profitable anymore. Population numbers then either stay very low or may slowly recover. MORA et al. (2007) summarized that overexploitation generally removes members from the stock population beyond natural levels of replenishment, reducing the genetic diversity and the ability to adapt to other threats and causing direct populations declines.

To evaluate possible consequences of habitat degradation and overexploitation for the amphibian community it is important to know which habitat factors structure species assemblages (ERNST & RÖDEL 2005). Community ecology therefore focuses on how abiotic processes, such as disturbance, affect biodiversity and how biotic factors, such as competition or predation, affect biodiversity dynamics (NAEEM et al. 2002).

Several factors influencing the composition of an amphibian community have been discussed with a lately main emphasis on environmental and spatial effects (e.g. PARRIS 2004, ERNST & RÖDEL 2008, HILLERS et al. 2008, KELLER et al. 2009). Local species pools and biotic processes such as dispersal strategies and abilities may lead to similar species composition in habitats, which are in close proximity (HECNAR & M'CLOSKEY 1996). On the other hand, the occurrence of particular species within a community may depend on various biotic and abiotic factors. HEYER et al. (1975) pointed out that tadpole species occurrence in any habitat is the result of the interactions of both physical (e.g. ponds dry up) and biotic parameters. In regard to controphic insect larvae, tadpole species for instance compete with mosquito larvae. They can either negatively affect mosquito larvae directly through interference and/or predation (e.g. *H. occipitalis* tadpoles prey on mosquito larvae), or indirectly through exploitation of shared resources, or even positively affect mosquito larvae by reducing predation on mosquito larvae by serving as alternative prey (BLAUSTEIN & CHASE 2007). As mosquitoes serve as vectors for various diseases such as Malaria, an investigation of this interaction is thus motivating.

West African amphibians probably play an essential role for the functioning of West African freshwater habitats and alterations of their communities may consequently alter entire ecosystems (MOHNEKE & RÖDEL 2009). It is therefore necessary to examine the relationship between environmental conditions and amphibian assemblage composition in the first place and in the following to examine the affect of the community composition on ecosystem function (see Chapter 6).

Herein I investigate tadpole communities of ephemeral ponds in a West African savanna region. The ponds were situated in two study sites in Burkina Faso, one, where frogs were collected and traded for the local markets, and the other one, where frogs were consumed occasionally and only rarely traded on markets. Both study sites contained two different disturbance regimes. The disturbed regimes included freshwater ponds in and around villages, where agriculture and livestock herding is intense and where frogs are collected for the local food market (MOHNEKE et al. 2010). The undisturbed regimes included freshwater ponds in protected areas, where it is officially prohibited to harvest wildlife.

The main questions addressed were: (1) are there differences in tadpole community compositions between disturbance regimes in general and between study sites due to differences in the level of frog harvest? (2) Do habitat factors correlate with tadpole assemblages? (3) Are changes of tadpole assemblages in disturbed areas a consequence of habitat alteration, or of (4) frog-harvesting? (5) Do tadpole assemblages affect co-occurring mosquito larvae assemblage composition?

5.2 Material and Methods

5.2.1 Study sites

The survey of natural ponds took place in the provinces of Ganzourghou and Gourma in Burkina Faso. Ganzourghou is situated in the centre and Gourma in the southwest of the country. The whole study region is characterized by a Sudanian climate with one rainy season lasting from April to October and an annual precipitation between 700 and 900 mm (precipitation data from the years 1990-99, see Wittig et al. 2007). The vegetation of the area is a mosaic of various types of grass, shrub and tree savannas. This region is, as well as the whole country, affected by an increasing human population. Large parts are cultivated with the main crops being corn, millet and cotton. Livestock farming, including cattle, goats, and sheep occurs in all accessible parts of the country.

We surveyed a total of 63 ponds in the two study regions (Fig. 5.1). To search for differences in tadpole compositions in relation to disturbance regimes, we surveyed ponds in disturbed areas (in and around villages) and in undisturbed areas (protected areas, reserves in each study region). In Gourma we surveyed 17 ponds in and around villages, most of which were located south of Fada N'Gourma (disturbed area) and another 15 in the Reserve de Pama (undisturbed area). In Ganzourghou we surveyed 16 ponds in and around Mogtedo and neighbouring villages (Zam and Kabouda; disturbed area) and another 15 ponds in the Reserve de Wayen (undisturbed area). The surveys were carried out during the rainy seasons of the years 2007 and 2008. In both years the rainy season started late, and most temporary ponds were not filled with water until mid July. As we planned to survey the ponds twice, at the beginning and at the end of the rainy season, we carried out one survey in the beginning of August and another at the end of September. Each survey followed the same standardized methodology.

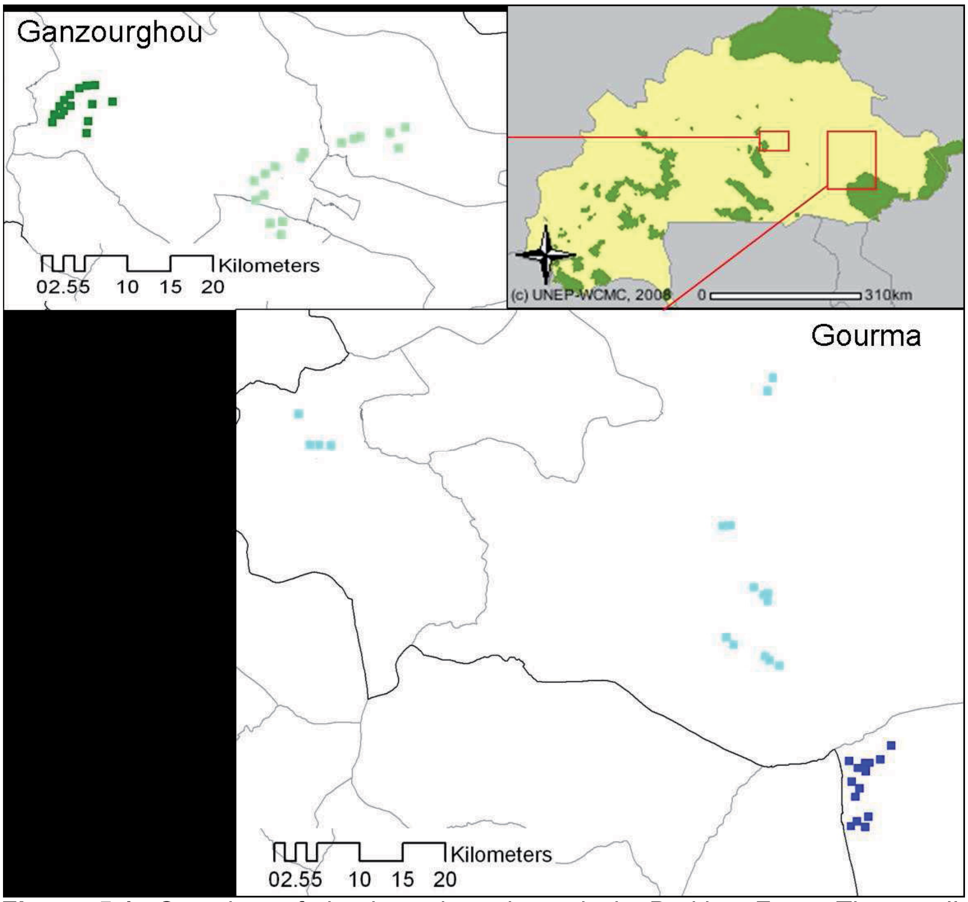


Figure 5.1. Overview of the investigated ponds in Burkina Faso: The small picture shows the country, Burkina Faso, and its protected areas (marked in green). Red squares show the study areas and detailed maps indicate the positions of the study ponds and the respective disturbance regime. Every dot symbolizes one pond. The colour of the dot symbolizes the study site with green= Ganzourghou and blue= Gourma. The colour intensity symbolizes the disturbance regime, with dark= undisturbed and light= disturbed.

5.2.2 Data collection

We investigated the composition of tadpoles and mosquito larvae communities in each study pond. For the sampling of tadpoles and mosquito larvae we followed a standardized method by applying the box method. A metallic box (height x width x length = 50x50x50 cm), which was open at top and bottom, was thrown into the pond. The water level inside the box was measured for calculating the water volume of the sample and consecutively tadpole density. The percentage of vegetation cover of the water surface inside the box was estimated and recorded (usually aquatic plants; accuracy of estimation ± 10%).

Mosquito larvae were sampled first to be sure to disturb them as little as possible. Therefore, we waited for app. 5 minutes, which allowed the water to calm and the mosquito larvae to return to water surface. The box was approached carefully and three consecutive dips were taken with the help of a standard WHO mosquito dipper (350 ml volume, see BECKER et al. 2003 for more information on this technique). The dipped water got poured into a white dish, where all larvae stages could be easily seen and counted. Fourth instars and pupae were collected and stored in 90% ethanol for further identification. The tadpole sampling followed the mosquito sampling. The water content inside the box was searched for tadpoles by using a plastic sieve. Only when in 10 consecutive strokes no tadpole was caught, the sampling was stopped. Collected tadpoles got stored in 5% formaldehyde for further measurements and identification. Larger mosquito instars caught with the plastic sieve at the same time were also additionally collected for further identification. For more information on the box method see RÖDEL et al. (2009).

The number of samples per pond was determined by the number of distinct micro-habitats. We usually distinguished between the following micro-habitats: open water and shore zone, vegetation rich, vegetation less and without vegetation, shallow water and deeper water and respective combinations. Each micro-habitat was sampled by one box throw. Accordingly, large ponds usually offered a minimum of three samples and small ponds often only a maximum of two samples (surface size of ponds ranging from 2.5 up to 350 m²).

Due to relative short rainy seasons, particularly in 2007, many ponds were already desiccated by the end of September (33 desiccated ponds in September 2007 and 6 desiccated ponds in September 2008). The sample size was thus smaller for September than for August. Additionally, the number of reported species was very low for September in comparison to August. We therefore decided to concentrate only on the samples for August. In 2008 two ponds were already/still desiccated in August, which reduced the number of ponds to 61. I further treated the two surveys in August in the two consecutive years as repeats of the same samples and thus pooled the samples of 2007 and 2008. Since habitat parameters did not change much between years I used the mean value calculated from the two years for each habitat parameter.

For each pond physical and chemical parameters were recorded specifying the ponds habitat structure and its water characteristics. Concerning ponds' abiotic habitat factors, the following parameters were recorded: estimation of the encountered surface size (accuracy of estimate ± 10% of the estimated surface size (m²)), depth (cm), visibility (cm), estimation of shaded area (accuracy of estimation ± 10%), estimation of vegetated area (accuracy of estimation ± 10%), estimated macro algae content, and soil. For depth recording the deepest point of the pond was measured using a yardstick. Visibility was measured with the help of a secchi disc. The macro algae content that was visible on the water surface, was estimated and classified into four categories (1. absent; 2. low: 1-10% macro algae content, visible but not very abundant; 3. middle: 11-50% macro algae content; and 4. high: 51-100% macro algae content in pond). The soil content was classified as loam, clay, sand or laterite (four categories).

Temperature (°C), pH, conductivity (µs) and salinity (ppm) of the ponds' water were measured with a combo-tester of Hanna instruments (HI 98129, accuracy of measurement:

pH ± 0.05, EC ± 2% of measuring range). The concentration of oxygen, nitrate, phosphor, and ammonium in the water were analyzed with colorimetric tests from Macherey-Nagel (MN Visocolor Eco, measuring range: NO_3^-: 1-120 mg/l, PO_4^{3-}:0.2-5 mg/l, NH_4^+:0.2-3 mg/l, O_2: 1-10 mg/l).

The ponds' surrounding savanna ecosystem is important as habitat for adult amphibians and assumingly differed between the study sites due to unequal human activities. In anthropogenic disturbed areas, the amount of grass and of high grown grass in particular, can be lower due to livestock grazing and agriculture. The density of shrubs and trees is usually also lower in disturbed areas due to agriculture and the collection of fire wood. Therefore, the vegetation surrounding each pond was recorded in four directions (South, West, North, and East) directly at the ponds' edge (= S) and in 10 m, 20 m, 30 m, 40 m and 50 m distance, respectively. Six different classes of vegetation were distinguished: 1= grass up two 30 cm, 2= grass higher than 30 cm, 3= low grown bushes (up to 1 m), 4= high grown bushes, 5= trees (≥ 2 m height), 6= soil and 7= fields (in general, no distinctions between crops were made). At each 10 m stop, the coverage of every class was estimated (accuracy of estimation ± 10%) for an area of approximately 1m² around the recorder. For the analysis we calculated the mean of the four directions for every vegetation class at every distance step. As the surrounding vegetation did not considerably change by comparison between the different distances, we pooled 10 and 20 m distances data (= A) and 30, 40, and 50 m distances (= B). The pooling was also essential to reduce the number of variables in statistical analyses.

5.2.3 Statistical Analyses

All ponds, of which many were located far away from each other, had to be sampled in a short time frame. As an intensive sampling would have been very time consuming I decided to sample instead the different micro-habitats of each pond (see above: sampling according to ponds structure). Due to this sampling strategy no quantitative conclusions can be made for tadpole and mosquito assemblages. And although quantitative data were collected with the box methods, I reduced them to presence/absence data for analyses. However, the sampling of every encountered micro-habitat was a relatively safe method to collect the majority of the present fauna. By applying different sampling methods (box method and scooping) in ponds in the Pendjari National Park, we usually found most of the tadpole species that got caught by scooping also in the box in the different micro-habitats (M. Mohneke, unpubl. data).

Not all tadpoles could be identified to species level. Determination in these cases was restricted to genus level. Tadpoles of the genus *Ptychadena* that could not be identified on species level did not enter multivariate analyses because different *Ptychadena* species usually called at different ponds. Many *Ptychadena* species and in particular older larvae can however, be assigned to a particular species. These data were used for analyses. In the same way I treated tadpoles of *Afrixalus*. In contrast species of the genus *Phrynobatrachus* usually always used (calling males encountered) the same breeding ponds, hence I entered all tadpoles under their genus name rather than separate species for multivariate analyses. The same I did for *Leptopelis* tadpoles. Probably the majority of *Leptopelis* tadpoles were *L. viridis* since *L. bufonides* tadpoles are usually rare. In one of the ponds of the disturbed area in Ganzourghou only tadpoles of the genus *Ptychadena*, which could not be identified further, were found. I excluded this pond and thus reduced the number of ponds that entered multivariate analyse to N= 60.

Mosquitoes were found in 44 of the 61 ponds in August 2007 and 2008. Since this number of ponds included the pond described above, where only *Ptychadena* spp. was found, I consequently reduced the number of ponds that entered multivariate analyses to N= 43. Thus, analysis concerning mosquito communities were based on N= 43 ponds for multivariate analyses and N= 44 ponds for non-parametric tests. Hierarchical cluster analysis was applied to look for similarities and/or dissimilarities respectively in the distribution of amphibian and mosquito genera and the particular environmental parameters in their ponds and surroundings. The cluster analysis for tadpole species and mosquito genera were based on Jaccard distance measure, for presence absence data, and farthest neighbour method (McCune & Grace 2002, Leyer & Wesche 2007). For the clustering based on habitat parameters the Euclidean (pythagorean) distance measure and the Ward's method as linkage method was chosen. Euclidian distance measure is recommended with metric data and is advised to be used along with the Ward's method (McCune & Grace 2002, Leyer & Wesche 2007).

Correlations between recorded ponds parameters, ponds' surrounding vegetation structures and the presence of tadpole genera and furthermore the relationships between the presence of amphibian and mosquito larvae were tested with Mantel tests (in R program version 2.10.0, R Development Core Team 2009), non-metric multidimensional scaling (NMDS, in PC-ORD version 5.19; McCune & Mefford 2006), and regression analysis (in SPSS for Windows version 16.0.1, 2007).

Besides habitat characteristics that could possibly determine species composition, geographical distance between freshwater ponds could likewise determine species compositions with close ponds showing a higher similarity. To test if species assemblages rather correlated with geographical distances or with habitat characteristics I applied the Mantel test for both tadpole and mosquito assemblages. The Mantel test was used to evaluate the congruence of distance matrices of the study ponds, including species composition, habitat factors and geographic distances between the study ponds. Thus, Mantel tests were applied to pairwise control for the influence of similarity in ponds habitat structure (separate distance matrices: one of vegetation structure and one of ponds parameters) and ponds proximity (geographical distances) on the similarity among tadpole species assemblages (based on presence/absence data). The distance matrices of habitat factors (except geographical distance matrix) were based on Sørensen (Bray-Curtis) index and distance matrices of species presence/absence data were based on Jaccard index.

The NMDS was applied since it is the most generally effective ordination method for ecological community data (McCune & Grace 2002). I performed the NMDS to test for correlations between habitat parameters (ponds parameters and ponds' surrounding vegetation structure – analyzed separately) and presence and absence of tadpole species. Additionally, NMDS was performed to test for correlations between tadpole and mosquito assemblages.

For preliminary runs Jaccard distance measure was applied and settings as followed: maximum number of iterations= 250, instability criterion= 0.00001, starting number of axis= 6, number of real runs= 250. Resulting configurations were defined as starting coordinates in subsequent ordinations with application of the suggested dimensionality.

In regard of the graphical NMDS representation, species and habitat parameters contributed to the ordination axis to different degrees, expressed through linear (Pearson's r= parametric) and rank (Kendall's τ= nonparametric) correlations (McCune & Grace 2002). Vectors represented habitat parameters that had highest correlation with ordination axis and thus had the most influence on the projection of ponds and respective species assemblages. Angles and length of vectors indicated direction and strength of correlations, respectively.

NMDS were followed by a second step where a NMDS were performed without the species presence and absence values in order to obtain ordination scores for ponds, which were correlated only with habitat parameters. For the NMDS performed with environmental pond parameters and surrounding vegetation classes only, a 2-dimensional and 3-dimensional solution were found, respectively. The ordination scores resulting from the NMDS were used to subsequently perform a regression analysis to test for significant species-specific habitat requirements. Ordination scores for plots resulting from the NMDS were used as independent variables and tadpole genera presence/ absence data as dependent variables. As the dependent variables are nominal data a multinomial logistic regression analysis was used to test for which species a significant relationship with habitat characteristics existed.

I further tested for significant differences between study sites and between disturbance regime concerning tadpole and mosquito species occurrences and habitat factors. Since the recorded data were not normally distributed, we used nonparametric tests. Mann-Whitney-U tests and Chi-square tests were applied to test for differences in species distribution between different disturbance regimes. The occurrence of amphibian species and mosquito genera was compared between disturbed (villages) and undisturbed (protected) areas separately for the two provinces Gourma and Ganzourghou and consecutively for the whole study region. Those tests were carried out in the program R version 2.10.0 (R DEVELOPMENT CORE TEAM 2009).

5.3 Results

A total of 3495 individual tadpoles were collected from 63 different ponds in and around villages and in protect areas in Burkina Faso (see appendix 2 for coordinates for detected tadpole species), 3012 at the beginning of the rainy season and 472 at the end of the rainy seasons in 2007 and 2008. A total of 489 samples, i.e. box throws have been taken: 301 for the beginning of the rainy season and 188 for the end of the rainy season. The comparatively low number of collected tadpoles at the end of the rainy season was to some extent due to the high rate of desiccated ponds especially in 2007. In this year the rainy season was exceptionally short. Since beginning and end of rainy season were dissimilar in regard of tadpole numbers I only used the data collected in the beginning of the rainy season for further calculation. I on average recorded 7 tadpoles per sample with a range of 0-95 tadpoles per sample and 0.2 tadpoles per litre pond water with a range of 0-9.5 tadpoles per litre pond water. In total 19 different species could get identified. Tadpoles belonging to the genera *Kassina* and *Amietophrynus* could not be assigned to species level. Concerning tadpoles of the genera *Afrixalus*, *Leptopelis*, *Phrynobatrachus* and *Ptychadena* not all individuals could get identified on species level (see above). With regard to the genus *Leptopelis* a second species, *Leptopelis bufonides*, could potentially occur in the study region but was not recorded and/or identified in this study. Those tadpoles that could not be identified on species level were excluded or entered the analysis under their genus name (see statistical analyses for details).

A total of 3662 mosquito larvae were recorded from the same 63 ponds, 1193 at the beginning of the rainy season and 2469 at the end of the rainy season. These numbers include all four larval stages, of which a total of 854 4^{th} instars larvae were collected for further identification. In contrast to the tadpoles, the numbers of mosquito larvae were comparatively high at the end of the rainy season, despite the high rate of desiccated ponds. However, as I only used the early rainy season data for tadpoles the same strategy was applied for mosquitoes. On average 7 4^{th} instars mosquito larvae were collected with a range of 0-49 4^{th} instars per sample and 0.4 larvae per litre pond water with a range of 0-5.5 4^{th} instars larvae per litre pond water. The mosquito larvae were assigned to one of the following genera: *Aedes*, *Anopheles*, *Culex*, *Lutzia*, *Mansonia*, and *Mimomyia*.

5.3.1 Tadpole species composition concerning disturbance regime and study site

The approach of a non-metric multidimensional scaling (NMDS) was carried out to look for differences in tadpole species composition in the ponds of investigation. The NMDS revealed a projection of the ponds along two axes based on the presence of amphibian species (Fig. 5.2). Ponds which are situated close to each other by the NMDS consisted of identical or similar tadpole community compositions respectively. Amphibian species with major influence on ponds' projection are shown as crosses. The main finding of this analysis is a separation of ponds with regard to the disturbance regime and to the study region. Hence, tadpole assemblages seemed to be more similar within one disturbance area than between disturbance regimes and furthermore within one study site than between them. The separation between dissimilar tadpole assemblages is stronger between disturbance regimes than between study regions. In the graph of the NMDS most ponds of the undisturbed regime in Ganzourghou (dark green dots in Fig. 5.2) were particularly positioned in close proximity. In comparison, ponds of the undisturbed regime in Gourma seemed to be rather different in their tadpole community compositions but were also to a high proportion separated from ponds of the disturbed areas. *Hemisus marmoratus* was placed in proximity to ponds of disturbed regimes and particularly of ponds in the disturbed area in Gourma, where it mainly occurred. In contrast, *Leptopelis* and *Ptychadena tournieri* were placed in opposite direction and hence explained projection of ponds of the undisturbed regime in Ganzourghou. Other species with comparatively high explanatory values, *Phrynobatrachus*, *Ptychadena bibroni*, *P. tellini*, *P. trinodis, Hoplobatrachus occipitalis*, and *Amnirana galamensis*, seemed to likewise have mainly influenced the projection of ponds in the undisturbed area. However, stress values for the NMDS pointed out that the plot needs to be interpreted with some caution (Tab. 5.1). McCune & Grace (2002) emphasised that NMDS with a stress value between 10 and 20 can still correspond to a usable picture, but too much reliance should not be placed on the details of the plot.

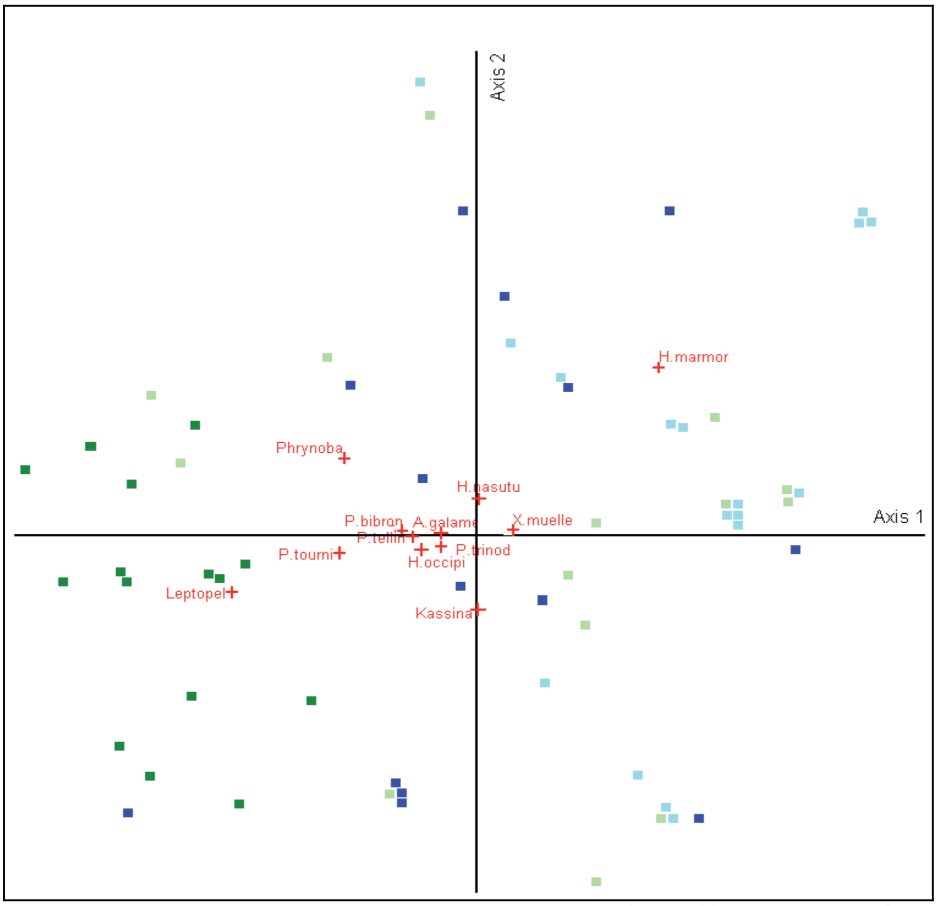


Figure 5.2. Non-metric multidimensional scaling (NMDS) ordination of the studied ponds (N= 60) of the whole study region. The positions of the ponds in the graph are determined by the presence and absence of tadpole species recorded in the ponds. Every colored dot symbolizes one pond. The colour of the dot symbolizes the study site with green= Ganzourghou and blue= Gourma. The colour intensity symbolizes the disturbance regime, with dark= undisturbed and light= disturbed. Crosses symbolize amphibian species with highest explanatory values for ordination axes. For species abbreviations see appendix.

Table 5.1. Stress values are shown for NMDS based on tadpole species composition in ponds. Stress values are given in relation to dimensionality (number of axis). Stress in real data and stress in randomized data based on Monte Carlo test are based on 250 runs respectively. The p-value is the proportion of randomized runs with stress less than or equal to the observed stress.

Axes	**Stress in real data**			**Stress in randomized data Monte Carlo test**			**p**
	Minimum	**Mean**	**Maximum**	**Minimum**	**Mean**	**Maximum**	
1	38.103	49.804	57.229	37.714	48.671	57.997	0.008
2	24.707	25.975	40.622	23.570	28.193	45.726	0.04
3	15.348	19.179	20.823	16.393	20.111	44.714	0.004

5.3.2 Tadpole species composition in relation to habitat factors

5.3.2.1 Tadpole species composition in relation to habitat factors and to geographical distances between ponds

So far, my results showed that tadpole communities between freshwater ponds were not identical and differed mainly between disturbance regime and to a lower extent between study sites. But which parameters are drivers for certain tadpole assemblages? Which environmental determinants are important in structuring particular tadpole communities?

Geographical proximity or distance could be a reason for similarity or dissimilarity of tadpole communities, respectively. In order to test for geographical distance as a reason for similarity or dissimilarity in tadpole species composition I applied the Mantel test (Tab. 5.2). Correlations between tadpole communities and geographical distances between ponds were significant meaning that ponds geographically closer to each other consisted of more congruent tadpole communities than ponds located further away from each other. Also, ponds surrounding vegetation and the environmental ponds parameters were positively correlated with geographical distances meaning that they are more similar within one study site and here more similar within one disturbance regime. Tadpole species compositions were significantly correlated with ponds surrounding vegetation and environmental ponds parameters. Thus, differences of tadpole species occurrences between the two study sites could be potentially due to the geographical distance between them and / or to vegetation structures and pond parameters.

Table 5.2. Pairwise Mantel Test to evaluate the congruence between two similarity matrices (matrices were based on tadpole species occurrences, ponds surrounding vegetation, environmental pond parameters, and the geographical distances between the ponds). Each matrix was based on the same set of sampled ponds (N= 60). The results are all significant, meaning that all matrices are positively correlated with each other. Given are the statistic r of Mantel and the level of significance (p).

Matrices compare	r	p
Species/ pond parameters	0.1873	0.001
Species/ surrounding vegetation	0.2185	0.002
Species/ geographical distance	0.1628	0.001
Pond parameters/ surrounding vegetation	0.1512	0.001
Pond parameters/ geographical distance	0.0537	0.023
Surrounding vegetation/ geographical distance	0.2096	0.009

5.3.2.2 Tadpole species composition in relation to mosquito genera composition

Geographical proximity or distance between ponds could be also a reason for similarity or dissimilarity regarding their mosquito larvae composition. To test for this possibility, I applied Mantel tests, i.e. to reveal potential correlations between mosquito species compositions and geographical distances (Tab. 5.3). I further tested for correlations between mosquito species compositions and tadpole species composition, and environmental pond parameters and ponds surrounding vegetation. The respective distance matrixes contained the number of ponds (N= 43) where mosquito larvae were found.

Mosquito composition only showed a trend towards a significant positive correlation with tadpole species compositions. There was neither a correlation between mosquito assemblages and geographical distances between ponds nor between mosquito assemblages and habitat factors. Hence, mosquitoes seemed to rather occur independently of disturbance regimes and of habitat factors but may be slightly correlated with tadpole assemblages.

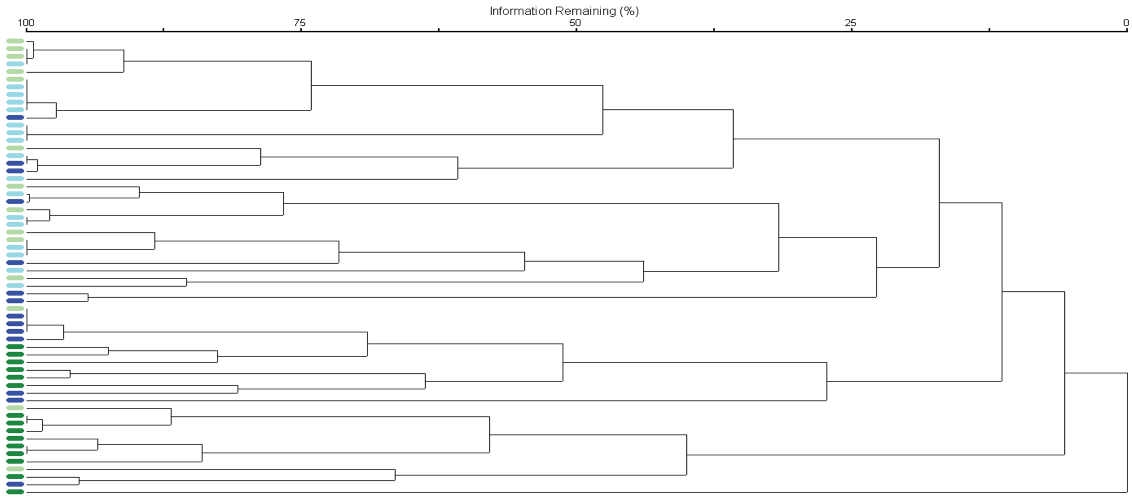
Table 5.3. Pair-wise Mantel test to evaluate the congruence between two distance matrices (matrices were based on mosquito genera occurrences, tadpole species occurrences, ponds surrounding vegetation, environmental pond parameters, and the geographical distances between the ponds). Each matrix was based on the same set of sampled ponds (N= 43). Given are the statistic r of Mantel and the level of significance (p).

Matrices compared	r	p
Tadpole species/ mosquito genera	0.0936	0.058
Mosquito genera / pond parameters	0.0467	0.267
Mosquito genera/ surrounding vegetation	0.0474	0.239
Mosquito genera/ geographical distance	0.0350	0.127

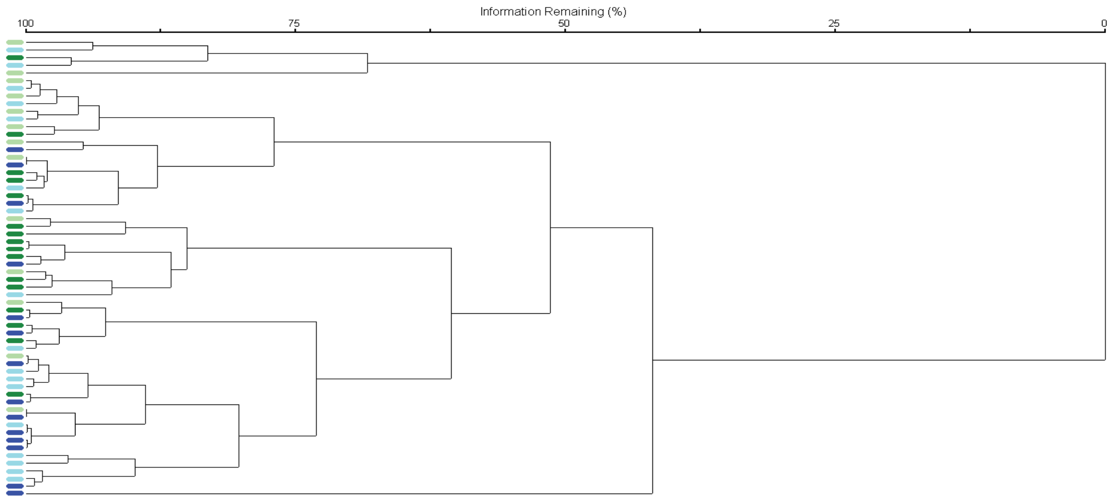
5.3.2.3 Comparisons between tadpole species composition and ponds environmental parameters and surrounding vegetation

Although the geographical distance between ponds correlated with the composition of tadpole species, the Mantel test gave no information concerning the different disturbance regimes. I conducted cluster analysis based on tadpole species composition, environmental ponds parameters and the ponds surrounding vegetation, respectively. In case tadpole species composition depends solely on habitat factors, I would assume three congruent cluster dendrograms resulting from these variables. Figure 5.3 shows those three cluster dendrograms (trees) resulted from respective cluster analysis. The investigated ponds (N= 60) are arranged in clusters regarding their similarity or dissimilarity in a) tadpole species composition, b) environmental pond parameters, and c) ponds surrounding vegetation. Concerning the tadpole species composition there was again a grouping based on disturbing intensity visible (Fig. 5.3a). The cluster analysis based on the ponds surrounding vegetation showed an even stronger grouping of ponds of undisturbed areas (dark symbols) and a grouping of ponds of disturbed areas (Fig. 5.3b). Ponds of the undisturbed area of Ganzourghou showed a strong grouping in particular, similar to tadpole assemblages. Thus, vegetation structure seemed to have been more similar around ponds in this area than in the other areas. The clustering of ponds based on the environmental pond parameters was different though (Fig. 5.3c) and is not as congruent with tadpole compositions and surrounding vegetation.

a) tadpole species composition



b) environmental pond parameters



c) pond surrounding vegetation

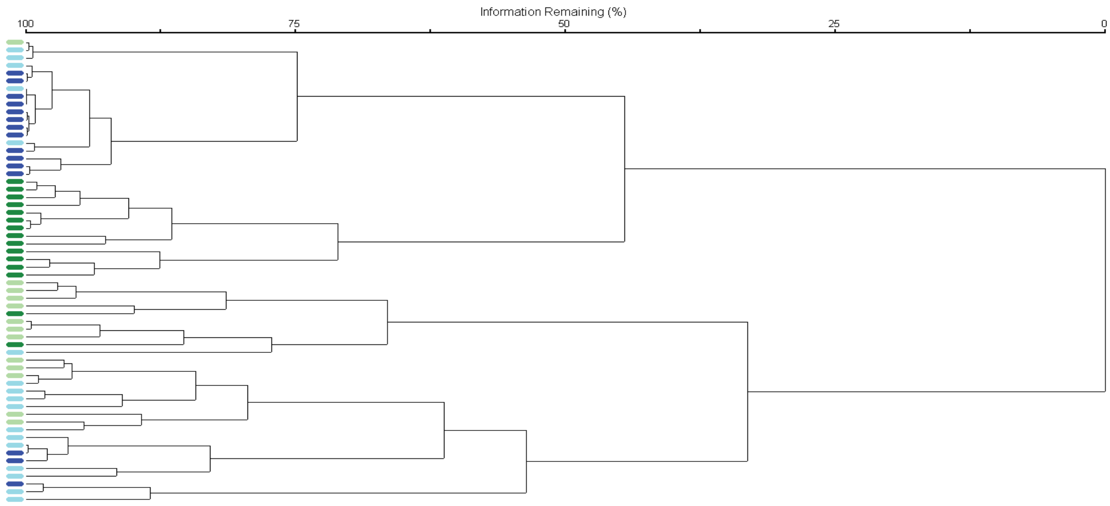


Figure 5.3. Results of three different cluster analysis: the investigated ponds (N= 60) are arranged in clusters regarding their similarity or dissimilarity in a) tadpole species composition, b) environmental pond parameters, and c) ponds surrounding vegetation. Every stripe symbolizes one pond. The colour of the stripe symbolizes the study site with green= Ganzourghou and blue= Gourma. The colour intensity symbolizes the disturbance regime, with dark= undisturbed and light= disturbed.

5.3.2.4 Comparison of mosquito genera composition and tadpole species composition

Since the Mantel test revealed a positive correlation between mosquito genera and tadpole species assemblages I conducted cluster analysis for those ponds, for which I could gain data of both tadpoles and mosquito larvae (N= 43). One cluster analysis was based on mosquito genera composition and one based on tadpole species composition (Fig. 5.4). In both cases ponds showed trends towards clusters according to disturbance regime (colour intensity). But, whereas for tadpole assemblages ponds of the undisturbed areas (dark

a) mosquito larvae genera

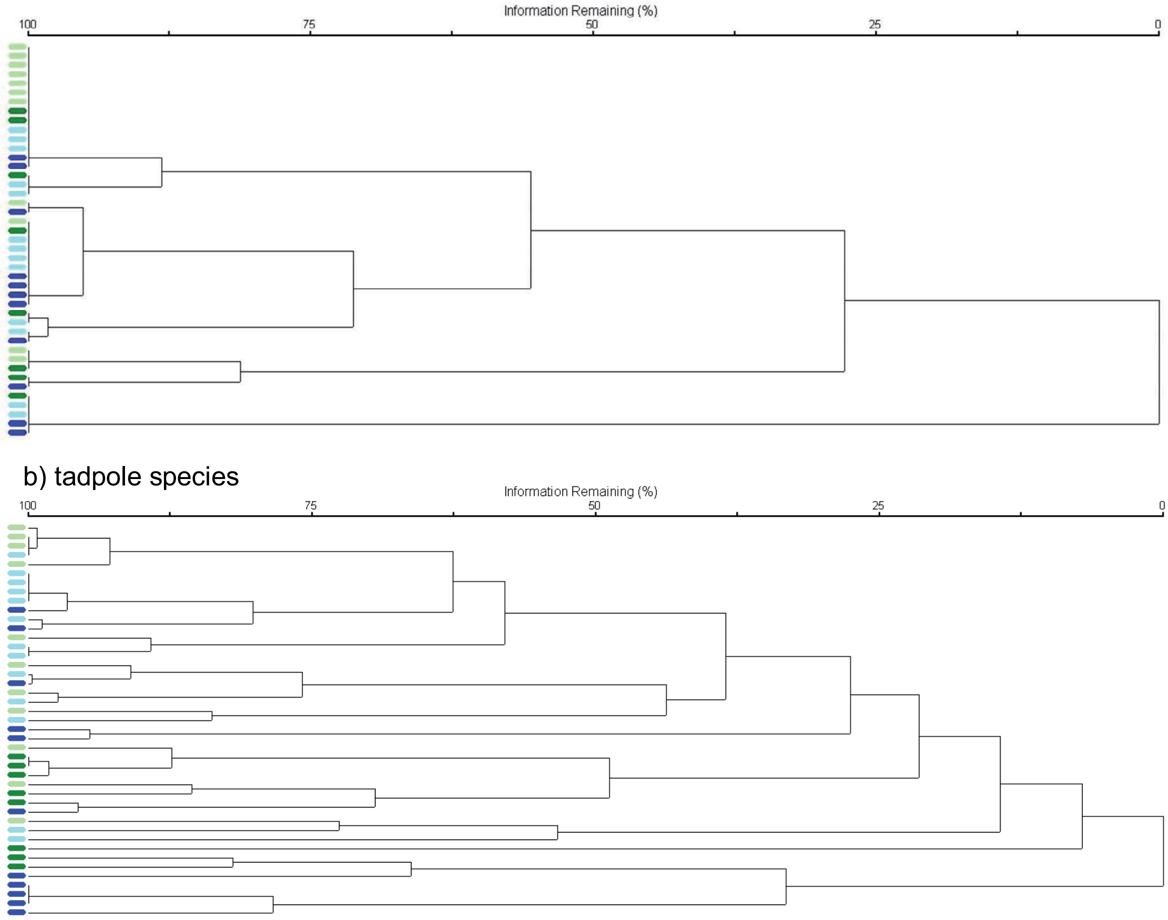


Figure 5.4. Trees resulting from cluster analysis with investigated ponds (N= 43) based on a) mosquito genera (5 genera) occurrences and b) tadpole species occurrences (20 species). Every stripe symbolizes one pond. The colour of the stripe symbolizes the study site with green= Ganzourghou and blue= Gourma. The colour intensity symbolizes the disturbance regime, with dark= undisturbed and light= disturbed.

symbols) were grouped (Fig. 5.4b), for mosquito assemblages rather ponds of the disturbed areas grouped (light symbols, Fig. 5.4a). Differences concerning the number of branches are due to a relative high number of tadpole species that entered the analyses compared to only 5 mosquito genera.

5.3.3 Frequencies of tadpole species and habitat factors in different disturbance regimes

5.3.3.1 Differences between disturbed and undisturbed sites concerning the tadpole compositions

Most of the recorded tadpole species showed differences in their frequency of occurrences between study sites and between disturbance regimes. Table 5.4 lists the absolute (number of ponds in which a species was detected) and relative frequency of occurrences for every recorded species for the two study sites (Ganzourghou and Gourma) and their two disturbance regimes. There is only one species, *Pyxicephalus edulis*, which is not listed since it was not caught with the box method. But a dense swarm of these tadpoles was observed in one of the studied ponds in a village in Gourma. Significant differences concerning tadpole's occurrences in disturbed and undisturbed areas were found for six out of 19 species (Tab. 5.5).

Only tadpoles of the genera *Kassina* and *Amietophrynus* occurred equally at all areas of investigation. The whole genus *Afrixalus* and the species *Hyperolius nasutus*, *Phrynobatrachus francisci*, *Ptychadena oxyrhynchus*, *P. tournieri* and *P. trinodis* were recorded in undisturbed areas only. *Afrixalus weidholzi* and *Phrynobatrachus latifrons* significantly more often occurred in undisturbed areas over the whole study region.

Ptychadena tournieri also occurred with a significant higher frequency in the undisturbed regime in Ganzourghou. In contrary, *Hemisus marmoratus* and *Xenopus muelleri* occurred with a significantly higher frequency at the disturbed sites in Ganzourghou. In Gourma, these two species also occurred more often in ponds of the disturbed area but differences were not significant here. *Leptopelis viridis*, showed significant differences for both study sites, with a higher frequency of occurrence in undisturbed areas. Likewise, *Leptopelis* spp. (including tadpoles that could not be determined on species level), which could potentially include *L. bufonides* besides *L. viridis*, occurred significantly more often in the undisturbed regime in Ganzourghou. *Phynobatrachus natalensis* and *Ptychadena oxyrhynchus* did not occur in Ganzourghou. In Gourma these two species were found in only one pond each, *P. natalensis* at the disturbed area and *P. oxyrhynchus* at the undisturbed area. In Gourma, seven species were not detected (*Amnirana galamensis*, *Hildebrandtia ornata*, *Leptopelis* spp., *P. francisci*, *Ptychadena bibroni*, *P. pumilio*, and *P. trinodis*).

Table 5.4. Recorded tadpole species with their absolute (a.f.) and relative (r.f.) frequency of occurrences at the two study sites and their respective disturbance regimes. The absolute frequency describes the number of ponds in which a species was detected and the relative frequency its respective proportion for the particular disturbance regime.

Tadpole Species	Ganzourghou				Gourma			
	Disturbed (N= 15)		Undisturbed (N= 15)		Disturbed (N=17)		Undisturbed (N=14)	
	a.f.	r.f. (%)	a.f.	r.f. (%)	a.f.	r.f. (%)	a.f.	r.f. (%)
Afrixalus spp.	0	0	2	13	0	0	1	7
A. vittiger	0	0	1	7	0	0	2	14
A. weidholzi	0	0	1	7	0	0	3	21
Amietophrynus spp.	1	7	1	7	1	6	1	7
Amnirana galamensis	1	7	2	13	0	0	0	0
Hemisus marmoratus	6	40	0	0	13	77	8	57
Hildebrandtia ornata	1	7	1	7	0	0	0	0
Hoplobatrachus occipitalis	1	7	5	33	1	6	0	0
Hyperolius nitidulus	1	7	1	7	0	0	3	21
H. nasutus	0	0	0	0	0	0	2	14
Kassina spp.	13	87	13	87	13	77	12	86
Leptopelis spp.	1	7	6	40	0	0	0	0
L. viridis	3	20	12	80	0	0	7	50
Phrynobatrachus spp.	4	27	5	33	2	12	3	21
P. latifrons	4	27	7	47	0	0	2	14
P. francisci	0	0	1	7	0	0	0	0
P. natalensis	0	0	0	0	1	6	0	0
P. microps	5	33	3	20	4	24	1	7
Ptychadena spp.	6	40	8	53	2	12	2	14
P. bibroni	2	13	5	33	0	0	0	0
P. oxyrhynchus	0	0	0	0	0	0	1	7
P. pumilio	3	20	2	13	0	0	0	0
P. tellini	1	7	5	33	1	6	0	0
P. tournieri	0	0	9	60	0	0	1	7
P. trinodis	0	0	2	13	0	0	0	0
Xenopus muelleri	5	33	0	0	3	18	0	0

In the disturbed area of Ganzourghou eight of 19 species were not detected, whereas five of 19 species were not present in the undisturbed area. In Gourma, 14 of 19 species did not occur in the disturbed area and ten of 19 species did not occur in the undisturbed area. These included the tadpoles of *Hoplobatrachus occipitalis*, which were not found in ponds in the undisturbed regime in Gourma. In Ganzourghou, however, these tadpoles showed a higher frequency of occurrences in the undisturbed regime. In the disturbed areas, this species occurred in only one pond at both study sites, respectively. Hence, species from various functional traits showed significant differences in their frequency between disturbance regimes. Those traits included filter-feeders such as *X. muelleri*, detritivors such as *H. marmoratus* and *Ptychadena* spp. and carnivors such *H. occipitalis*. Also, tadpoles belonging to tree and reed frogs such as *Lepopelis* spp, *Afrixalus* spp. and *Hyperolius* spp. likewise showed differences in their frequency between disturbance regimes.

Table 5.5. Comparison of frequency of occurrences of each recorded species between disturbed and undisturbed areas a) over the whole study region (N= 61) b) in Ganzourghou (N= 30) c) in Gourma (N= 31). Frequencies of occurrences were compared by applying the Mann-Whitney-U test. Given are the statistic (W) and the level of significance (p).

Tadpole species	Between disturbed and undisturbed in general		Between disturbed and undisturbed in Ganzourghou		Between disturbed and undisturbed in Gourma	
	W	**p**	**W**	**p**	**W**	**p**
Afrixalus spp.	416	0.067	98	0.164	111	0.3
A. vittiger	416	0.067	105	0.351	102	0.124
A. weidholzi	400	**0.033**	105	0.351	94	0.053
Amietophrynus spp.	461	0.933	113	1	118	0.926
Amnirana galamensis	431	0.266	105	0.577	111	0.300
Hemisus marmoratus	596	**0.028**	158	**0.008**	134	0.480
Hildebrandtia ornata	463	0.963	113	1	119	n.a.
Hoplobatrachus occipitalis	413	0.187	83	0.078	126	0.399
Hyperolius nitidulus	415	0.136	113	1	94	0.053
H. nasutus	432	0.140	113	n.a.	102	0.124
Kassina spp.	425	0.365	113	1	100	0.237
Leptopelis spp.	383	**0.034**	75	**0.036**	119	n.a.
L. viridis	188	**<0.001**	45	**0.001**	51	**<0.001**
Phrynobatrachus spp.	423	0.422	105	0.715	108	0.493
P. latifrons	362	**0.044**	90	0.275	94	0.053
P. francisci	448	0.309	105	0.351	119	n.a.
P. natalensis	479	0.358	113	n.a.	126	0.399
P. microps	515	0.322	128	0.433	130	0.543
Ptychadena spp.	420	0.427	98	0.487	116	0.864
P. bibroni	413	0.187	90	0.213	119	n.a.
P. oxyrhynchus	448	0.309	113	n.a.	111	0.300
P. pumilio	476	0.738	120	0.653	119	n.a.
P. tellini	413	0.187	83	0.078	126	0.399
P. tournieri	304	**<0.001**	45	**<0.001**	111	0.300
P. trinodis	432	0.140	98	0.164	119	n.a.
Xenopus muelleri	580	**0.004**	150	**0.018**	140	0.112

In general, the number of species per pond was significantly higher in the undisturbed areas than in the disturbed areas with respect to the whole study region (Mann-Whitney-U test, $W= 238.5$, $p< 0.001$, $N= 61$, Fig. 5.5a). The comparison of the number of species per pond between the four different sites revealed significant differences (Kruskal-Wallis test, $X^2= 20.801$, $df= 3$, $p< 0.001$, range= 1-10, mean= 4, $N= 61$, Fig. 5.5b). A pair-wise comparison (post-hoc Wilcoxon rank sum test) between each of the sites showed that significant differences existed between undisturbed and disturbed areas in both study sites and between the two study sites. Differences in species richness thus occurred between disturbance regime and between study sites.

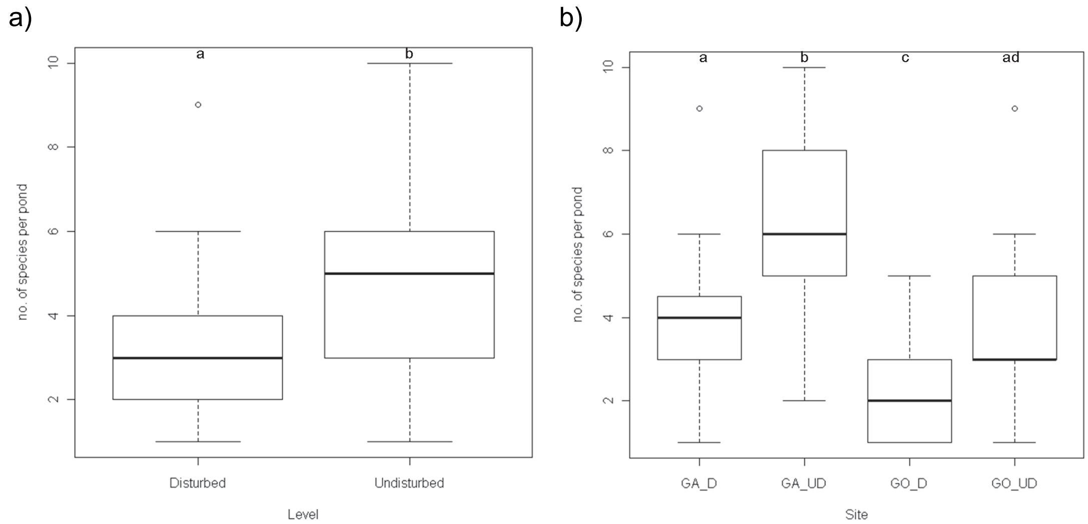


Figure 5.5. The median number of tadpole species per pond was compared between a) disturbed and undisturbed regimes including all investigated ponds (N= 61) and b) between the different disturbance regimes (D=disturbed; UD= undisturbed) for each study site (GA= Ganzourghou; GO= Gourma). Different small letters indicate significant differences between disturbance regimes and sites.

5.3.3.2 Differences of habitat factors between different disturbance sites

I assumed that habitat factors also differed in their values between disturbance regimes due to anthropogenic activities. These differences in environmental factors may have resulted in altered tadpole assemblages. Therefore, I tested each habitat factor, including the environmental pond parameters and the ponds surrounding vegetation classes, in regard of significant differences between disturbance regimes of the whole study region and for each study site separately (Tab. 5.6).

I found significant differences for ponds origin (man-made or natural), depth, turbidity, shade and soil concerning the whole study region. In Ganzourghou, significant differences were encountered for ponds origin, percentage of shade and soil type and in Gourma for ponds origin and ponds depth. Ponds in disturbed areas were significantly deeper. Turbidity was higher in undisturbed areas. A significantly higher percentage of shade was estimated for ponds in the undisturbed area. Regarding the different soil types, clay was recorded more often in ponds in undisturbed (30%) than in disturbed regimes (16%). This soil type particularly dominated in ponds in the undisturbed area in Ganzourghou (80% of ponds in undisturbed and 40% of ponds in disturbed area). In Gourma laterite showed a higher frequency in ponds in the disturbed area. Ponds with a sandy ground were only recorded in two ponds in disturbed areas.

Ponds in undisturbed regimes were exclusively of natural origin whereas 68% of ponds in the disturbed areas were of man-made origin. The latter ones were usually created by removing soil for house building (mainly clay) or road construction (mainly laterite). Parameters such as surface size, vegetation density, macro-algae content, pH, conductivity, ammonia, nitrate, phosphate and oxygen consecutively differed not significantly between study sites.

Table 5.6. Habitat factors (environmental pond parameters and ponds surrounding vegetation), which were recorded for every pond, were compared between disturbed and undisturbed areas over the whole study region and for each study site separately (Mann-Whitney-U test). Abbreviations for the different vegetation classes and the distances from the ponds where they were recorded are as follows: S= shore, A= in 10-20 m distance, B= in 30-50 m distance; 1= grass up two 30 cm, 2= grass higher than 30 cm, 3= low grown bushes, 4= high grown bushes, 5= trees, 6= soil and 7= fields. Significant differences are marked in bold. Given are the statistic (W) and the level of significance (p).

Habitat Factors		**Whole study region: disturbed/ undisturbed**		**Ganzourghou: disturbed/ undisturbed**		**Gourma: disturbed/ undisturbed**	
Environmental ponds parameters		**W**	**p**	**W**	**p**	**W**	**p**
Ponds origin		160	**<0.001**	45	**<0.001**	35	**<0.001**
Surface		347	0.091	73	0.105	98	0.415
Depth		228	**<0.001**	66	0.054	57	**0.015**
Turbidity		621	**0.024**	143	0.213	165	0.071
Shade		605	**0.039**	168	**0.021**	124	0.853
Vegetation		563	0.157	115	0.950	165	0.074
Macroalgae		512	0.485	102	0.674	152	0.189
Soil		290	**0.007**	66	**0.028**	78	0.089
PH		416	0.493	91	0.373	133	0.605
Conductivity		361	0.139	109	0.885	85	0.177
Ammonia		384	0.244	104	0.721	88	0.211
Nitrate		440	0.723	100	0.613	115	0.884
Phosphate		518	0.438	106	0.785	160	0.107
Oxygen		343	0.070	79	0.144	90	0.246
Ponds surrounding vegetation							
Distance	**Vegetation class**						
S	1	469	0.947	115	0.95	115	0.884
S	2	518	0.44	129	0.506	133	0.606
S	3	370	0.067	108	0.81	77	**0.017**
S	4	541	0.165	133	0.306	135	0.424
S	5	654	**0.001**	179	**0.004**	147	0.088
S	6	408	0.118	113	1	91	0.061
S	7	450	0.358	113	n.a.	112	0.399
A	1	275	**0.006**	81	0.191	57	**0.013**
A	2	740	**< 0.001**	186	**0.002**	199	**0.002**
A	3	344	0.077	52	**0.01**	125	0.839
A	4	678	**0.002**	153	0.095	191	**0.004**
A	5	790	**< 0.001**	212	**< 0.001**	167	0.062
A	6	360	0.094	75	0.079	104	0.507
A	7	276	**<0.001**	53	**0.002**	84	**0.033**
B	1	326	**0.046**	93	0.419	60	**0.018**
B	2	783	**< 0.001**	199	**<0.001**	219	**< 0.001**
B	3	318	**0.027**	60	**0.027**	91	0.232
B	4	676	**0.002**	139	0.278	223	**< 0.001**
B	5	872	**< 0.001**	211	**< 0.001**	212	**<0.001**
B	6	347	0.075	86	0.261	80	0.104
B	7	93	**< 0.001**	23	**< 0.001**	25	**< 0.001**

Concerning the ponds surrounding vegetation significant differences between disturbance regimes were detected for high and low grass, high and low shrubs, and trees. There were higher percentages of these three vegetation classes in undisturbed areas. Only low shrubs were recorded significantly more often at ponds in the disturbed area. In contrary to the soil type of the ponds ground, the soil type of the surroundings did not significantly differ between disturbance regimes.

Tadpole assemblages correlated with habitat factors (see above results from Mantel test). Those habitat factors that showed significant differences in their values between disturbance regimes could thus potentially have been responsible for differences in presence and absence of certain tadpole species in the respective disturbance areas and hence for alterations in tadpole assemblages in disturbed areas.

5.3.3.3 Differences between disturbance regimes concerning mosquito assemblages

In a total of N= 44 ponds mosquito larvae were detected and collected including 19 ponds in undisturbed areas (8 ponds in Ganzourghou and 11 ponds in Gourma) and 25 ponds in disturbed areas (12 ponds in Ganzourghou and 13 ponds in Gourma).

Five different mosquito genera could be distinguished, with *Culex* showing the highest frequency of occurrence followed by *Anopheles*, *Aedes* and *Lutzia* and *Mimomyia*.

A comparison of the frequency of occurrences of the collected mosquito genera between disturbance regimes (Tab. 5.7) revealed that *Culex* was recorded with higher frequencies of occurrences in disturbed areas but this difference was not significant. Larvae of *Anopheles* and *Aedes* occurred more often in ponds of undisturbed areas, but significant differences were found for *Aedes* in Ganzourghou only. In Gourma, however, *Aedes* were found more often in disturbed areas. The genus *Mimomyia* occurred solely in the disturbed area with a significant differences regarding its frequency of occurrences between disturbance regimes in Gourma.

Table 5.7. Frequency of mosquito genera were compared between disturbed and undisturbed areas over the whole study region and for each study site separately (Chi-squared test). Significant differences are marked in bold. Given are the statistic (X^2) and the level of significance (p).

Mosquito genera	Whole study region: disturbed/ undisturbed (N= 44)		Ganzourghou: disturbed/ undisturbed (N= 20)		Gourma: disturbed/ undisturbed (N= 24)	
	X^2	p	X^2	p	X^2	p
Aedes	2.800	0.094	**30.414**	**< 0.001**	1.220	0.270
Anopheles	3.306	0.069	3.482	0.062	2.946	0.086
Culex	0.973	0.324	1.044	0.307	0.911	0.340
Lutzia	0.111	0.739	n.a.	n.a.	0.059	0.809
Mimomyia	0.111	0.739	**8.000**	**0.005**	**9.000**	**0.003**

5.3.4 Tadpole species compositions correlating with habitat factors

Occurrences of certain tadpole species and certain habitat factors differed between disturbance regimes. But how are tadpole species compositions and habitat factors correlated? A nonmetric multidimensional scaling (NMDS) revealed projections of the investigated ponds (N= 60) based on their characteristic tadpole communities (Fig. 5.6). As in Figure 5.2 ponds with similar tadpole species composition were located in close proximity. Additionally, habitat factors with major influence in ponds projection are shown as vectors. I carried out two different NMDS one considering the environmental pond parameters and tadpole species occurrences and a second considering ponds surrounding vegetation classes and tadpole species occurrences. In both cases a three-dimensional ordination was produced due to lower stress-levels (Tab. 5.8). In the first case (considering environmental pond parameters) the three axis explained together 78.3% of overall variance (axis 1: 33.9%, axis 2: 22.7%, and axis 3: 21.7%) and in the second case (considering surrounding vegetation classes) the three axis explained 78.3% of overall variance (axis 1: 15.7%, axis 2: 40.9%, and axis 3: 21.7%).

Among environmental ponds parameters with highest correlation values (depth, shade, concentration of ammonia, nitrate, and phosphate, conductivity, and pH) depth seemed to mainly explain projection of ponds of Gourma and shade rather ponds of Ganzourghou, particularly of the undisturbed regime. Projection of ponds of the undisturbed regime in Ganzourghou was influenced by nitrate concentration and estimated vegetation cover. In contrast, phosphate concentration rather influenced the projection of ponds of disturbed regimes. Agricultural activity in the disturbed regimes could have been a reason for that.

In regard of the ponds surrounding vegetation, highest correlation values were revealed for trees, high grass, and high shrubs and for bare soil in all three distance categories respectively. Trees at shore, in 10-20m and in 30-50m distance were mainly responsible for projection of ponds of Ganzourghou and here of the undisturbed regime in particular. The undisturbed area in Ganzourghou was characterized by tree savanna vegetation which also explained the high correlation values of shade. Outliers such as ponds of disturbed areas (ponds in light colours in Fig. 5.6) that are situated in proximity to ponds of the undisturbed area (ponds with dark colours in Fig. 5.6) were also characterized by a comparatively high amount of trees and shrubs and consequently high amount of shade.

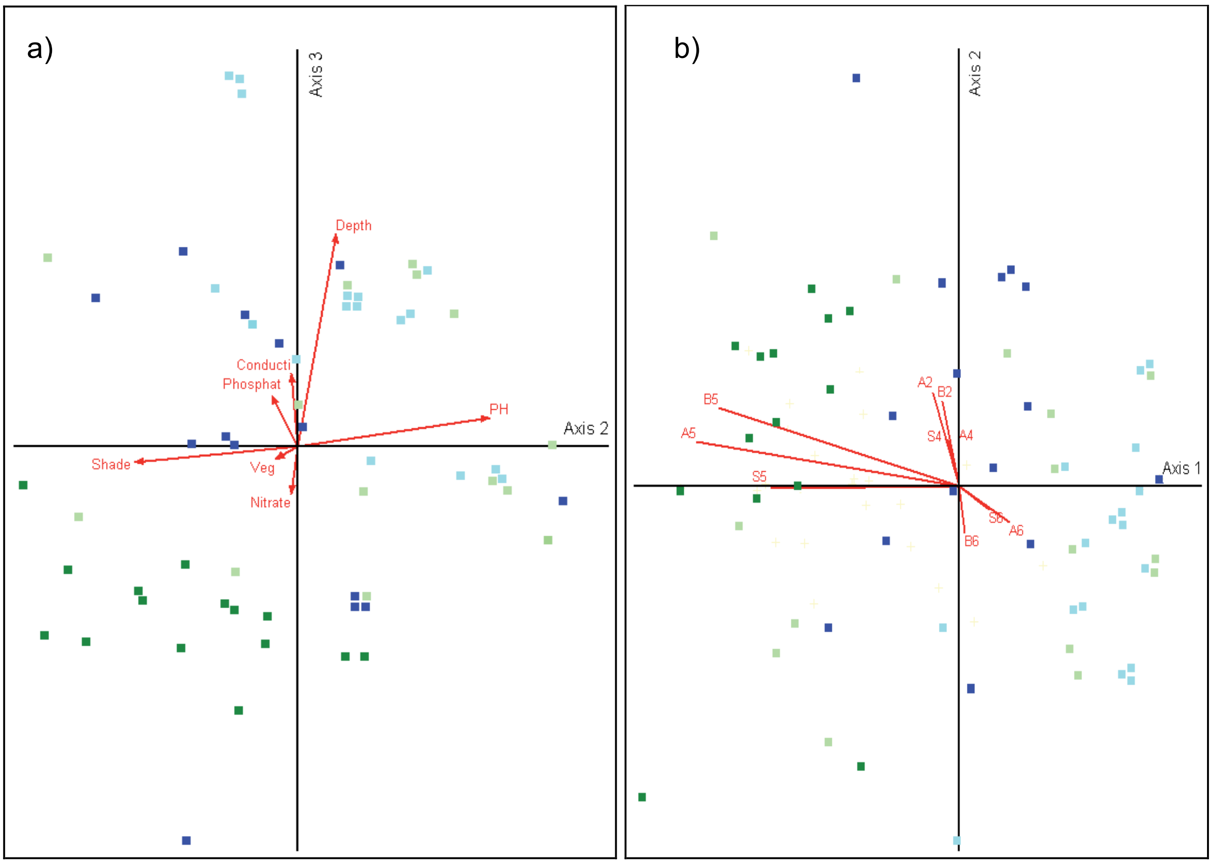


Figure 5.6. Nonmetric multidimensional scaling (NMDS) ordination of the investigated ponds (N= 60) and their respective tadpole species composition. The projection of the ponds is determined by a) environmental pond parameters, which were recorded in the ponds and b) the ponds surrounding vegetation classes. Every dot symbolizes one pond. The colour of the dot symbolizes the study site with green= Ganzourghou and blue= Gourma. The colour intensity symbolizes the disturbance regime, with dark= undisturbed and light= disturbed. Vectors describe abiotic factors with highest explanatory values for ordination axes. For abbreviations see appendix; for abbreviations of vegetation classes see 5.2.2 data collection

Table 5.8. Stress values for NMDS based on environmental pond parameters and on ponds surrounding vegetation classes. Stress values are shown in relation to dimensionality (number of axis). Stress in real data and stress in randomized data based on Monte Carlo test are based on 250 runs respectively. The p-value is the proportion of randomized runs with stress less than or equal to the observed stress.

Variables	Axis	Stress in real data 250 runs			Stress in randomized data Monte Carlo test, 250 runs			p
		Minimum	Mean	Maximum	Minimum	Mean	Maximum	
Environmental pond parameters	1	´38.126	50.182	57.080	35.919	48.874	58.443	0.012
	2	24.708	26.137	40.626	23.583	28.221	44.541	0.072
	3	15.339	19.246	21.196	15.846	19.719	47.762	0.004
Vegetation structure parameters	1	38.109	49.081	57.115	35.904	49.033	58.072	0.008
	2	24.701	25.923	40.623	23.872	27.900	53.420	0.04
	3	15.347	19.197	20.798	16.013	19.922	40.666	0.004

The following NMDS with habitat parameters alone revealed a 2-dimensional solution for environmental pond parameters and a 3-dimensional solution for surrounding vegetation classes. The corresponding regression analysis with ordination scores obtained with these NMDS showed significant correlations between environmental pond parameters and the tadpole species *Kassina* spp. (r^2= 0.175; p= 0.002), and *Hoplobatrachus occipitalis* (r^2= 0.077, p= 0.032), and between surrounding vegetation classes and *Hemisus marmoratus* (r^2= 0.089, p= 0.025) and *Amietophrynus* spp. (r^2= 0.254, p= 0.001). Whereas *Kassina* spp. and *Amietophrynus* spp. occurred with equal frequencies in the different disturbance regimes, the other two species showed differences in their rate of occurrences between disturbance regimes. Altered habitat factors in disturbed areas could thus have been a reason for a decline (*H. occipitalis*) or increase (*H. marmoratus*) respectively of these species. However, as *H. occipitalis* is known to be unselective in its choice of habitat and occurs in a broad range of different water bodies and environment, it is unlikely that these altered habitat factors led to the decline of this species in disturbed areas.

5.3.4.1 Mosquito composition in relation to tadpole composition

There were differences between disturbance regimes in regard of the respective recorded mosquito genera. The mosquito genera only correlated with tadpole species occurrences and respective cluster trees were partly congruent (congruence in colour intensity). A non-metric multidimensional scaling (NMDS) was applied to examine how presence and absence of mosquito genera influenced the projection of investigated ponds (N= 43). Furthermore, presence and absence of tadpole species in relation to mosquito larvae assemblages are shown. A two-dimensional ordination was suggested (see Tab. 5.9 for stress values) and the two axes explained together 97.5% of overall variance (axis 1 53.9% and axis 2 43.7%; Fig. 5.7). The ponds were again partly separated based on the disturbance regime. But ponds of disturbed areas were stronger accumulated than ponds of undisturbed areas. The three dominating genera, *Aedes*, *Anopheles* and *Culex* showed an opponent influence. Hence, there seemed to be usually one dominating genus of mosquito larvae in freshwater ponds in the study region (Fig. 5.7). Tadpole species with highest explanatory values are shown as crosses in Figure 5.7. Larvae of the genus *Culex* seemed to co-occur with species that showed higher occurrence rates in disturbed areas, such as *Amnirana galamensis*, *Xenopus muelleri*, *Hemisus marmoratus*, *Ptychadena pumilio*, *Kassina* spp., and *Leptopelis*. Larvae of the genus *Anopheles* predominantly correlated with *Ptychadena bibroni* and *Hyperolius nitidulus*.

A second NMDS without the mosquito values could not be performed since a useful NMDS configuration was not found.

Table 5.9. Stress in relation to dimensionality (number of axis) of NMDS based on mosquito and tadpole assemblages. Stress in real data and stress in randomized data based on Monte Carlo test are based on 250 runs respectively. The p-value is the proportion of randomized runs with stress less than or equal to the observed stress.

Axis	Stress in real data 250 runs			Stress in randomized data Monte Carlo test, 250 runs			p
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	
1	28.726	50.267	56.406	24.233	47.891	59.716	0.143
2	6.427	23.241	40.070	10.841	24.961	40.067	0.048
3	2.652	19.229	30.671	3.989	10.540	42.227	0.048

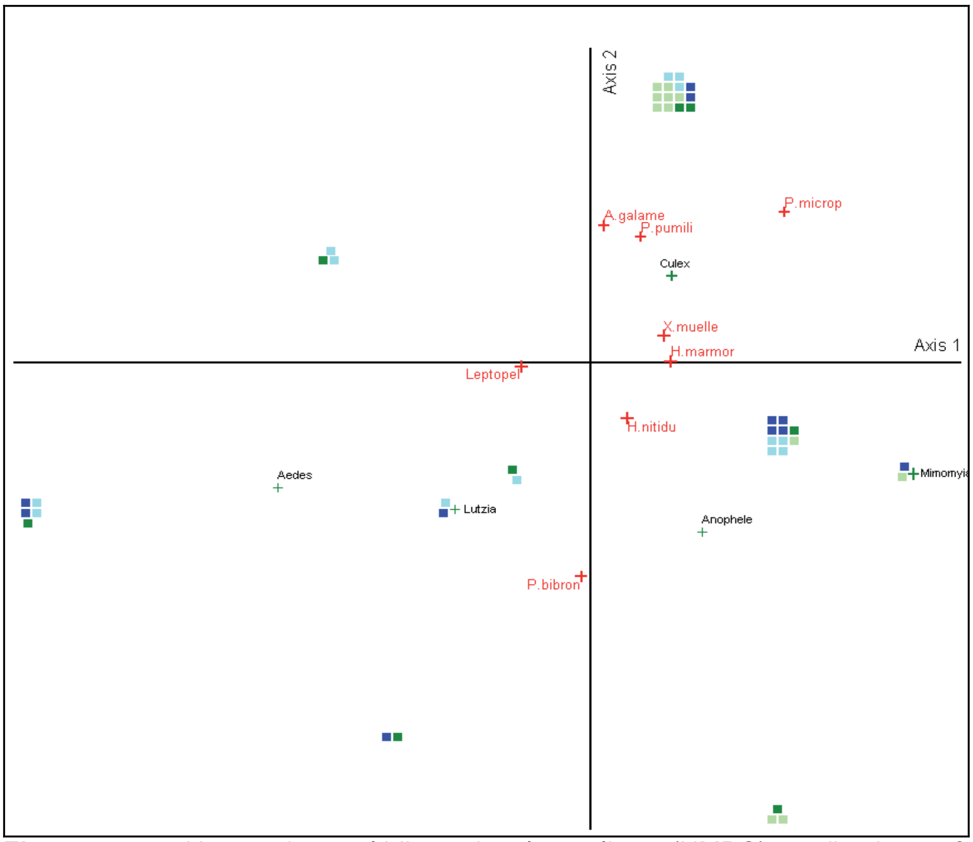


Figure 5.7. Nonmetric multidimensional scaling (NMDS) ordination of investigated ponds, where mosquito larvae were recorded (N= 43). The positions of the ponds in the graph are determined by the presence and absence of mosquito genera (dependent variables) and the presence and absence of tadpole species (independent variables). Crosses describe species with highest explanatory values for ordination axes. Every dot symbolizes one pond. The colour of the dot symbolizes the study site with green= Ganzourghou and blue= Gourma. The colour intensity symbolizes the disturbance regime, with dark= undisturbed and light= disturbed. For species abbreviations see appendix.

5.4 Discussion

5.4.1 Tadpole species composition in relation to disturbance regime and respective habitat factors

This study aimed to compare tadpole communities between disturbed and undisturbed areas and thus to investigate correlations between different tadpole communities and particular abiotic and biotic factors. Tadpole communities clearly differed between disturbance regimes. One major finding was a lower species number of tadpoles in anthropogenic disturbed areas, which was also reported in other studies on amphibian communities (HECNAR & M'CLOSKEY 1996a, LETHINEN et al. 1999, HERRMANN et al. 2005, BELL & DONNELLY 2006, CUSHMAN 2006, ERNST et al. 2007). ERNST & RÖDEL (2008) and HILLERS et al. (2008) reported lower species richness, abundance, and diversity in amphibian communities in disturbed (fragmented) areas of West African rainforest. Accordingly, ERNST & RÖDEL (2005) found a decrease in total number of species when comparing primary with selectively logged forest in Central Guyana, South America. Often habitat alterations in disturbed sites were said to lead to declines in amphibian species numbers and reduced communities down to broad-scale habitat tolerant members (ERNST & RÖDEL 2008). With regard to leaf-litter frog assemblages in West Africa, several frog species were lost in disturbed (logged) rainforest areas because canopy opening resulting in micro-climatic changes, posed physiological constraints onto the amphibian communitiy (ERNST & RÖDEL 2005, ERNST et al. 2006, HILLERS et al. 2008). Habitat alterations were probably also a reason for lower species richness in disturbed areas in this study. Species such as *Afrixalus*, *Hyperolius*, and *Leptopelis viridis* that depend on terrestrial vegetation could be affected by livestock grazing or also by habitat degradation such as logging of trees and shrubs for firewood. By removing trees, shrubs and tall grasses, the calling sites of these species were destroyed. Consequently ponds in disturbed areas, where these vegetation features were not existent anymore, were no longer used for breeding by these species.

The composition of tadpole species also differed between disturbed and undisturbed areas similar to other studies (HECNAR & M'CLOSKEY 1996, BELL & DONNELLY 2006, ERNST & RÖDEL 2008, HILLERS et al. 2008). ERNST & RÖDEL (2008) assumed that spatial effects were of prime importance in structuring amphibian community composition. They found that sites that were geographically proximal tended to have similar communities due to dispersal colonization processes. In my study, areas of different disturbance regimes were in direct proximity hence spatial effects were actually thought to be of minor importance. Instead habitat alterations probably led to altered tadpole assemblages in disturbed areas. Anthropogenic disturbance have acted for a very long time, which could have resulted in long-term changes of amphibian assemblages in these areas. Agriculture and livestock farming have long been carried out in these areas but traditional cultivation has shifted towards intensive cropping and pasturing due to human population growth (BATIONO et al. 1998, SÖDERSTRÖM et al. 2003). Amphibians are known to be particularly sensitive to agricultural land use (SEMLITSCH 2000) due to pesticide application, sedimentation and fertilizer run off (RELYEA 2005). Additionally, livestock graze shorelines and terrestrial vegetation and deposit nitrogenous waste in these areas (SCHMUTZER et al. 2008). Differences in tadpole assemblages could hence be due to long term agrarian impact.

The cluster analysis gave indication that the surrounding vegetation could have been more important for tadpole community compositions than the measured habitat factors concerning breeding ponds. By representing the habitat of adult amphibians, the surrounding vegetation might have played an important role for the composition of tadpole communities.

A number of habitat factors correlated with tadpole community compositions and hence could play a role in determining the occurrence of certain tadpole species. Former studies likewise suggested that amphibians are choosing ponds on the basis of their average environmental characteristics (e.g. VAN BUSKIRKS 2005, KELLER et al. 2009). Some of these factors (depth, turbidity, shade, soil type and the amount of grass, shrubs, and trees) differed in their values between disturbance regimes (appendix 3 provides pictures of pond examples from every disturbance regime). Those parameters might be influenced by different configurations of the respective habitats due to varying human activity (tree cutting might be responsible for less shaded ponds in disturbed areas, removal of certain soil types such as laterite for construction of roads etc. might be responsible for a higher frequency of laterite as pond bottom and deeper ponds in disturbed areas). In case human activity altered a specific habitat factor, it could subsequently alter the frequency of a tadpole species in a disturbed area (HECNAR & M'CLOSKEY 1996a, BABBITT et al. 2003, HERRMANN et al. 2005).

The amount of trees in the surrounding habitat of ponds correspondingly correlated with tadpole species but it also differed significantly between disturbance regimes with lower tree density in disturbed areas. Tall grass and shrubs also differed between disturbance regimes. These habitat structures are important for African tree frogs. Accordingly, tadpoles of *Leptopelis*, *Hyperolius*, and *Afrixalus* showed differences in their presence in disturbed and undisturbed areas. Species such as *Afrixalus vittiger* and *A. weidholzi* exclusively occurred in undisturbed areas. *Leptopelis*, *Hyperolius nitidulus* and *Hyperolius nasutus* also occurred more often in undisturbed areas. *Leptopelis* influenced the projection of ponds of the undisturbed area in Ganzourghou in the NMDS based on tadpole species. Adults of *L. viridis* usually stay buried underground during the day and come out during the night to climb up trees (RÖDEL 2000). Calling males usually sit elevated on trees or high shrubs. Hence, the occurrence of this species could potentially be correlated with the amount of available calling sites i.e. trees and shrubs. However, calling sites can be situated far away from the next water pond and this species is even characterized as synanthropic (RÖDEL 2000).

Adults of *Xenopus muelleri* and *Hoplobatrachus occipitalis* usually stay along rivers edges during the dry season and start to migrate long distances into the savanna after the first rain falls (RÖDEL 2000, SPIELER & LINSENMAIR 1998). Hence, the surrounding habitat of their breeding ponds not necessarily represented the whole adult habitat. Distance to the next river or to a permanent waterbody could have been more important in explaining their occurrences. A lack of such permanent water sources could be therefore one reason for the absence of *H. occipitalis* and *X. muelleri* in the undisturbed area in Gourma. *H. occipitalis* significantly correlated with environmental pond parameters as regression analysis revealed. ERNST et al. (2006) and HILLERS et al. (2008) have also assumed that water persistence could be negatively influenced by forest degradation and could have led to a loss of amphibian pond specialists in disturbed areas. SPIELER & LINSENMAIR (1997) hypothesized that water holding capacity of ponds is an important parameter for oviposition in *H. occipitalis* besides avoiding pools with conspecifics and higher densities of tadpoles in general. The water holding capacity was said to be determined by the rate of evaporation (ratio of surface area to depth) and exposition of a pond. The latter parameter could be represented by the percentage of shade and the densities of trees along the ponds edge. Depth and shade were also two parameters with significant differences between disturbance regimes. Due to a higher percentage of trees and accordingly shade above ponds in the undisturbed area in Ganzourghou, ponds might be characterized by a higher water holding capacity due to less exposure to direct sunlight and thus less evaporation. This could be a general reason for the high species richness in this area compared to the other investigated sites. Accordingly, *H. occipitalis* were found most often in this area. In contrast, shade has been found to negatively correlate with species richness in temperate zones (FICETOLA & BERNARDI 2004, WERNER et al. 2007). In an unstable savanna habitat with strong fluctuating hydroperiods, shade thus seems to become important for a better water holding capacity of ponds and accordingly for species occurrences. On the other hand, trees may draw off water from the ponds with their roots especially when they stand close to ponds' shore lines. However, my personal observation was that ponds without shade dried off faster than ponds surrounded by trees and shrubs. Besides providing shade, vegetation further creates diverse habitats, moderates temperature, retains moisture and contributes to organic matter (in HERRMANN et al. 2005). Furthermore, soil type of ponds' ground could influence the amount of water loss by seepage. Water holding capacity of ponds has been found to be one of the main parameters for choosing suitable oviposition sites in tadpoles by several studies (e.g. HEYER et al. 1975, SCHNEIDER & FROST 1996, SKELLY 1997, SPIELER & LINSENMAIR 1997, RUDOLF & RÖDEL 2005, WERNER et al. 2007). I would also assume that water persistence is of similar importance for tadpole occurrences in ponds of the study region. Differences of parameters that could potentially determine water holding capacity of a pond (surface, depth, shade, soil type) between disturbance regimes could subsequently influence the tadpole composition. Species with longer duration of larvae development would thus be assumed to positively correlate with water persistence like for example *H. occipitalis*. However, besides *H. occipitalis* only *Kassina* spp. significantly correlated with environmental pond parameters indicating that either most tadpoles occurred independently of these abiotic habitat factors or the recorded habitat parameters were not relevant for the majority of species.

Despite a lower species number in general, there were also species that exclusively occurred in disturbed areas. *Xenopus muelleri* occurred exclusively in disturbed areas in both study sites. *Hemisus marmoratus* occurred only in the disturbed area in Ganzourghou. In Gourma, *H. occipitalis*, *Ptychadena tellini* and *Phrynobatrachus natalensis* were found exclusively in the human dominated area. Other studies on amphibian communities also reported of species that were associated with disturbed sites and were not recorded in undisturbed regimes (HECNAR & M'CLOSKEY 1996a, PEARMAN 1997, ERNST & RÖDEL 2008, HILLERS et al. 2008). The species with higher occurrence rates in disturbed areas belonged to different genera and have a different biology, which could be a hint that tadpole assemblage structures depended not only on habitat factors. *H. marmoratus* adults live most of the time underground. Therefore, it would probably not depend on specific, dense vegetation structures, which were more present in undisturbed areas. This independence of vegetation structures could have been an advantage as this species could occur in disturbed areas where less amphibian species co-occurred, and thus with less competition about resources and breeding habitats. However, surrounding vegetation classes were significantly correlated with *H. marmoratus*. Soil moisture depends on vegetation and could be an important habitat factor for amphibians that live underground as *H. marmoratus*. The fact that this species were found more often in the disturbed area with less natural vegetation shows that it is rather independent of specific vegetation structures. Since the surrounding vegetation classes included the proportion of fields, short grass (often due to grazing), and bare soil around ponds, *H. marmoratus* may as well have correlated with those factors being more common in disturbed areas.

Water chemistry parameters did not show significant differences in their concentrations between disturbance regimes and sites. Non-metric multidimensional scaling revealed that pH, conductivity and nitrate concentration correlated with tadpole species composition with pH and conductivity predominantly correlating with tadpole species composition in disturbed areas and nitrate concentration correlating with tadpole composition in the undisturbed area in Ganzourghou. Surprisingly, nitrate concentration had an influence in the projection of ponds of the undisturbed regime in Ganzourghou. I would have assumed that this parameter is rather correlated with ponds of disturbed regimes due to livestock herding and agriculture. However, neighbouring villagers sometimes used to herd their cattle inside the Reserve de Wayen, which could have led to higher nitrate concentrations in the respective ponds Wildlife such as larger mammals has been wiped out in Wayen as in most reserves in Burkina Faso except in the south-east like in the Reserve de Pama (undisturbed area in Gourma). A few ponds in the Reserve de Pama also showed very high nitrate values. Fresh elephant tracks in and around these ponds indicated that those high values were probably based on high urine concentrations in these ponds. Hence, a high nitrate concentration is not necessarily an indicator of disturbance. Generally, the savanna ecosystem is an unpredictable environment, characterised by high temperatures, unpredictable rainfalls and larger mammals (wildlife and/or domestic animals), which appear in more or less irregular intervals. Hence unpredictable changes of certain habitat factors are part of the tadpoles' ecosystem and species that live in this environment should be able to coop with naturally changing habitat factors. Nitrate concentrations in ponds for instance can increase over a very short time due to the urination of large mammals such as elephants (or cattle). I would therefore assume that this parameter has no influence in the occurrence of savanna tadpole species. Likewise, HECNAR & M'CLOSKEY (1996b) pointed out that water chemistry is not important in explaining the presence and absence of amphibian species in North America. Accordingly, BEEBEE (1985) and PAVIGNANO et al. (1990) found that water chemistry parameters such as pH and hardness were not significant predictors of amphibian presence and absence in Europe. Since, abiotic parameters were not of significant importance for the presence and absence of amphibian species in ponds in a tropical savanna habitat (this study) as well as in temperate zones this might be a general rule. Rather non-chemical pond characteristics and the surrounding habitat are important predictors of amphibian occurrences.

5.4.2 Tadpole species composition in relation to mosquito species composition

Anopheles and *Culex* larvae are primarily filter feeders, consuming phytoplankton, whereas many *Aedes* and *Culiseta* mosquito larvae are primarily periphyton feeders (STAV et al. 2005, MATTHYS et al. 2006, BLAUSTEIN & CHASE 2007). Hence they might be sharing similar trophic levels with tadpoles. Tadpoles are known to compete with mosquito larvae (BLAUSTEIN & MARGALIT 1994, MOKANY & SHINE 2002a) and predatory tadpoles such as the larvae of *Hoplobatrachus occipitalis* are known to prey on mosquito larvae (NOPPER 2010). These interactions could possibly affect tadpole and mosquito larvae assemblages vice versa (BLAUSTEIN & CHASE 2007).

Mosquito larvae composition differed between disturbance regimes with *Culex* showing a higher rate of occurrence in disturbed areas and *Aedes* and *Anopheles* in undisturbed areas.

Based on my results these differences could not be explained with habitat alterations but with altered tadpole assemblages. Mosquito assemblages were dominated by usually one of the three genera (*Aedes*, *Anopheles* and *Culex*). Species-specific interactions could have been possible and usually compassed larvae of one mosquito genera and co-occurring tadpole species. Such species-specific interactions have been found for mosquito larvae (*Culiseta longiareolata*) and tadpoles of the green toad (*Bufo viridis* in BLAUSTEIN & MARGALIT 1994, 1995, 1996) and for the mosquito larvae of *Culex quinquefasciatus* and *Ochlerotatus australis* and the competing tadpole species, *Limnodynastes peronii* and *Crinia signifera* (MOKANY & SHINE 2003a, b).

Tadpole species with highest explanatory values, regarding mosquito assemblage compositions, included species like *Phrynomantis microps, Kassina* spp. and *Amietophrynus* spp., which did not show differences in their occurrence between disturbance regimes but are likely competing with mosquito larvae over the same food sources. Only *P. microps* tadpoles showed a higher occurrence rate in disturbed areas among those species. These tadpoles are heavily preyed upon by *H. occipitalis* tadpoles (see chapter 6). Hence, the lower occurrence rate of *H. occipitalis* in disturbed areas could be an advantage for *P. microps* tadpoles. In turn, their presence as competitors could possibly be a disadvantage for mosquito larvae. *Phrynomantis microps* and *Xenopus muelleri* tadpoles are filter-feeders and likely competed with *Anopheles* and *Culex* larvae due to their filter-feeding activities. *Anopheles* larvae might have been disadvantaged in this competition, which could have led to their low presence in disturbed areas. In that case, alterations of tadpole assemblages in anthropogenic disturbed areas could have even been an advantage for the local human population. *Aedes* and *Anopheles* larvae were both found less often in the disturbed areas. A lower presence of *Anopheles* and *Aedes* mosquitoes in and around villages could subsequently lower the rate of diseases such as Malaria or Dengue fever that get transmitted to humans via these mosquito species.

Grazing (*Kassina*) tadpoles could indirectly positively affect filter-feeding mosquitoes because herbivores could confer advantage to groups of algae such as phytoplankton by reducing competitive ability of the plant (e.g. for nutrients, UV-radiation) and by recycling nutrients (BLAUSTEIN & CHASE 2007). In fact, *Kassina* spp. and *Culex* larvae have both been found in vegetation rich micro-habitats of ponds. Detritivourous tadpoles such as *Hemisus marmoratus* could have a positive affect by open up nutrition by their detritivorous feeding activities. This could play a role in ponds of the disturbed areas, where these tadpoles co-occurred with *Culex* larvae.

However, differences in mosquito assemblages could also be explained by species specific life-history traits (CHASE & SHULMAN 2009). Some *Culex* species are known to breed in smaller water bodies (e.g. containers, puddles) whereas *Anopheles* species are known to be better dispersers and in comparison with *Culex* rather exclusive pond/wetland breeders (CHASE & SHULMAN 2009). Hence, the higher occurrence rate of *Culex* in disturbed areas could be explained by a range of different suitable breeding habitats (various small water bodies in villages) in the neighbourhood of the studied ponds and proximity to higher density of hosts. Such small breeding habitats were not abundant in undisturbed areas as well as human hosts.

This study revealed significant correlation between tadpole and mosquito larvae assemblages. In contrast no correlations were found between mosquito assemblages and habitat factors or geographic distances between freshwater ponds. It is therefore possible that mosquito larvae assemblages were rather determined by biotic interactions than by abiotic habitat factors. However, an effect of mosquito assemblages on tadpole species composition is possible but not proven. Former studies reported that abiotic factors are more important in influencing tadpole assemblages than biotic factors (e.g. HEYER et al. 1975, SCHNEIDER & FROST 1996, LEHTINEN et al. 1999). SCHNEIDER & FROST (1996) postulated that abiotic factors could determine the presence and absence of species and patterns of abundance were caused by biotic interactions. Since reliable abundance data could not be obtained for tadpole and mosquito larvae, no statement concerning patterns of abundance caused by biotic interactions can be made.

5.4.3 Factors besides habitat factors affecting tadpole assemblage compositions

Besides the lower total number of species in disturbed areas compared to undisturbed areas, the total number of species was lower in Gourma than in Ganzourghou. General environmental differences between the two sites could have led to differences in species richness. Amphibian species richness is ultimately determined by environmental factors that affect colonization and extinction (HECNAR & M'CLOSKEY 1996a). The analysis based on the Mantel test revealed significant correlations between tadpole species composition, habitat factors and geographical distances. Hence, ponds with close proximity to each other had a higher similarity in their tadpole species compositions than ponds further away from each other. This is in accordance with ERNST & RÖDEL (2008) and HILLERS et al. (2008), where arboreal frog and leaf-litter frog assemblages respectively were spatially structured, i.e. sites in close proximity had similar species assemblages. Differences in tadpole species occurrences between the two study sites (Ganzourghou and Gourma) could be explained by different species pools (HECNAR & M'CLOSKEY 1996a), from which the local tadpole communities recruited their members. As habitat factors also correlated with geographic distances, different parameter values could support occurrences of different species, which resulted in different species pools in the two study sites. There were tadpole species that were found in one of the two study sites only. In total six different species were exclusively found in Ganzourghou and three species were found in Gourma only (Tab. 5.4), which argues for different species pools at the two study sites. Studies that examined amphibian assemblages in regard of spatial and environmental effects revealed different results. ERNST & RÖDEL (2006, 2008) and HILLERS et al. (2008) stated that spatial structure is of major importance, whereas environmental effects were affecting assemblages only in degraded habitats. KELLER et al. (2009) found environmental parameters of most importance in structuring amphibian stream assemblages. Likewise, PARRIS (2004) detected major environmental and minor spatial effects on anuran species composition. In our case, spatial and environmental effects seemed to act together in structuring tadpole species composition. Both study sites are characterized by the same Sudanian climate and tree savanna ecosystem. But Ganzourghou is more affected by a higher density of human population and villages and agricultural activity than Gourma. Its close proximity to the capital Ouagadougou probably led to a higher development rate in comparison to Gourma, the poorest and most underdeveloped province of Burkina Faso. Due to this higher pressure of anthropogenic impact I would have assumed lower species richness in Ganzourghou. Data on environmental changes (e.g. intense agriculture, climate changes), which may explain a recent loss of diversity are not available. Based on the available information it is more likely that the species pool in Gourma differed from the one in Ganzourghou. Species that were not encountered in Gourma are *Amnirana galamensis*, *Hildebrandtia ornata*, *Ptychadena bibroni, P. pumilio*, *P. trinodis*, and *Phrynobatrachus francisci*. Tadpoles of these species usually occur solitary and in low abundances, hence I might have missed to detect them with the box method. Especially in larger ponds, where the number of box throws was proportional low; those tadpole species could have occurred but were not detected. But, although I might have missed a species in one pond, the large number of sampled ponds per study site and disturbance regime ensured to detect all species present in one area. There was usually a time difference of seven days between the start of the survey in Gourma and the start of the survey in Ganzourghou. Species that breed early in the rainy season, like *Hildebrandtia ornata*, could have been thus missed at the site that was surveyed later in the season. I always surveyed ponds in Gourma first and ponds in Ganzourghou afterwards. Tadpoles of species that usually breed later in the season, like *Afrixalus*, have been encountered in ponds in Gourma only (the study site I visited earlier in the rainy season) and tadpoles of *H. ornata* have been encountered in ponds in Ganzourghou only. Therewith, it is ensured that I detected early and late breeding species at both study sites.

Whereas spatial effects possibly explained differences in recorded tadpole assemblages between study regions, environmental effects seemed to play roles in structuring tadpole assemblages between disturbance regimes. WERNER et al. (2007) concluded that amphibian community assembly is a function of both local and regional factors, where local environmental heterogeneity is associated with variation in species richness due to disturbance gradients among others.

However, not all differences in tadpole species composition and occurrences of particular species could be explained with habitat factors. Besides spatial and environmental effects, harvesting of adult frogs could have had a direct negative effect on species occurrences. In MOHNEKE et al. (2010) we reported an increasing trade of frogs in Ganzourghou, in contrast frogs were consumed rather occasionally in Gourma. Hence, I would have assumed that species richness is higher in Gourma. The exploitation predominantly concerned *Hoplobatrachus occipitalis* followed by *Pyxicephalus edulis*, *Ptychadena bibroni*, *P. oxyrhynchus* and *P. trinodis*. Tadpoles of *P. edulis* were not encountered in the investigated freshwater ponds except one swarm was observed in one of the ponds in the disturbed area in Gourma. Among the species that get harvested, *H. occipitalis*, *P. bibroni*, *P. pumilio* and *P. trinodis* had lower rate of occurrences in the disturbed area in Ganzourghou. These differences in occurrence rates between disturbance regimes could be potentially due to the harvest of these species.

Among the species, which were not encountered at all in Gourma, *Ptychadena bibroni*, *P. pumilio*, and *P. trinodis* were also used for consumption. Hence, their absence in Gourma could have been due to low abundances and consequently difficulties in detecting these species during our study. But since harvesting rates were lower in this study site, I assume that their low rate of occurrences was not due to harvesting but could be possibly due to non-suitable habitat characteristics and/or climatic conditions.

Pyxicephalus edulis (see above) and *Ptychadena oxyrhynchus* were solely found in Gourma, with *P. oxyrhynchus* only occurring in the undisturbed area. Higher harvesting intensity in Ganzourghou could possibly explain their absence in this study site. But their overall low rate of occurrence and abundance could have led to difficulties in detecting those tadpoles.

In general, harvesting of adult amphibians could have affected tadpole composition by taking specific species out of the environment in high numbers. This especially concerns *Hoplobatrachus occipitalis*. Tadpoles of *H. occipitalis* are top-predators in freshwater ponds' food webs (RIEMANN 2010). Hence, their decline could further affect the occurrences and abundances of remaining tadpoles (higher survival rates but probably also higher rates of competition). Changes in tadpole assemblages could potentially also affect assemblages of co-occurring invertebrates such as mosquito larvae assemblages (MORIN 1988, KIFFNEY & RICHARDSON 2001).

In order to predict the consequences of alterations in tadpole communities it is necessary to investigate the biological function of tadpole species. To examine the effects of the loss of specific tadpole species we carried out an experimental approach, which will be described in the next chapter.

6 Ecological role of tadpoles – Species exclusion experiments in artificial ponds

6.1 Introduction

Tadpoles are important and integral components of freshwater ecosystems worldwide. Generally, they can play important roles as consumers (MCDIARMID & ALTIG 1999), but also are important as prey for various taxa (e.g. dragonfly larvae, water beetles, fishes, turtles, and birds; HERO et al. 1998, RÖDEL 1998). The general opinion has been that tadpoles are omnivorous and feed unselectively (SEALE 1980, MCDIARMID & ALTIG 1999). Only few studies have demonstrated that they are indeed capable of choosing food that varies in quality (KUPFERBERG 1997, BABBITT & MESHAKA 2000). A recent study by SCHIESARI et al. (2009) identified tadpoles as opportunistic feeders and pointed to a complex trophic interaction in ponds' food webs. Depending on their respective feeding strategy and trophic level, tadpoles are interacting with co-occurring species, and can affect ecosystem processes. Several studies have outlined their role in freshwater habitats by altering algal assemblages, patterns of primary production, and organic matter dynamics (e.g. KUPFERBERG 1997, FLECKER et al. 1999, RANVESTEL et al. 2004). Concerning predatory tadpoles, they are known to function as both intraguild predators and cannibals (HAWLEY 2009). They could be potentially very effective in structuring tadpole communities by directly influencing survival rates as has been shown for newt (ALFORD 1989) and salamander larvae (MORIN 1983). But proofs of anuran tadpole species being predatory have only been reported recently (as for bullfrog larvae; SCHIESARI et al. 2009). Furthermore, predation can relieve competition by decreasing prey densities and can thus improve the prospects of competitively inferior species (MORIN 1983, WILBUR 1987). For example *Hyla crucifer* and *Hyla gratiosa* are two species that relied on predators to reduce competition among tadpoles and ensure their larval success (MORIN 1983). In other cases, shifts in feedings strategies, such as shifts to different food resources, seemed to be possible under resource competition. For example, SEALE (1980) observed that grazing tadpoles reduced the availability of suspended particles, which led to some tadpoles switching to marginal, less nutrient-rich food source such as the sediments under high tadpole densities.

Both intra- and interspecific competition and density-effects can determine growth rates of tadpoles (WILBUR 1997). Additionally, food quantity and quality can also have an impact on growth and development of tadpoles (KUPFERBERG 1997). This, in turn, can affect the time it takes the larvae to obtain the minimum size for metamorphosis, which can be crucial particularly in temporary ponds. Various studies have investigated the mutual affects between tadpole species on growth (WILBUR & COLLINS 1973, MORIN 1983, WILBUR 1987,

WERNER & ANHOLT 1996, BARDSLEY & BEEBEE 2000, KATZMANN et al. 2003, RICHTER-BOIX et al. 2007), development (MORIN 1983, WILBUR 1987, KATZMANN et al. 2003), and survival rates (MORIN 1983, WILBUR 1987, WERNER & ANHOLT 1996, BARDSLEY & BEEBEE 2000).
Furthermore, tadpole assemblages can potentially affect co-occurring taxa, such as mosquito larvae through direct or indirect effects. Regarding mosquito larvae assemblages, oviposition by female mosquitoes within ponds can be affected by competitors and predators (BENTLEY & DAY 1989, ANGELON & PETRANKA 2002, MOKANY & SHINE 2003c, KIFLAWI et al. 2003, BLAUSTEIN et al. 2004, ARAV & BLAUSTEIN 2006, BLAUSTEIN & CHASE 2007). Competition and predation can also directly affect growth, development, and survival of mosquito larvae and can thus determine mosquito larvae community structure (JENKINS 1964; BAY 1974; MARIAN et al. 1983; KÖGEL 1984; BLAUSTEIN et al. 1994; BLAUSTEIN & MARGALIT 1996, MOKANY & SHINE 2003b, KNIGHT et al. 2004, STAV et al. 2005, BLAUSTEIN & CHASE 2007, KESAVARAJU et al. 2008). Respectively, the presence of competitive tadpoles has been shown to severely influence mosquito population dynamics (MOKANY & SHINE 2003a). It is further possible that predatory tadpoles also directly influence mosquito larvae survival.
But although tadpoles play an important role in a variety of freshwater habitats, comparatively little is known about their part in tropical ecosystems in general and savanna habitats in particular. The majority of above mentioned studies dealt with anuran communities of temperate zones (e.g. WILBUR & COLLINS 1973, MORIN 1983, WILBUR 1987, WERNER & ANHOLT 1996, BARDSLEY & BEEBEE 2000). The investigated tadpole species usually occurred from species-poor systems and often were similar in their morphology. Assuming that morphological characteristics reflect specific trophic levels, these species were further similar in their function in the respective systems (STRAUß et al. 2010). In regard of tropical tadpole assemblages, STRAUß et al. (2010) encountered also a low functional diversity and functional redundancy but a high species richness in tropical streams. However, other tropical anuran communities appear rich in species richness and functional diversity (e.g. HERRMANN et al. 2005, HILLERS & RÖDEL 2007, HILLERS et al. 2009) including amphibian communities of West African savannas (RÖDEL 1998, 2000, NAGO et al. 2006)
In concern of West African savanna anuran communities, a current potential overexploitation of frogs could lead to a decreasing number of adult frogs and consequently to decreasing tadpoles densities in certain regions (see Chapters 2 and 3). Assuming complex trophic relationships, consequences with regard to the whole tadpole community are possible. An altered biodiversity may further affect ecosystem properties and functioning, including ecosystem services which might be of importance to humans (LOREAU et al. 2001, HOOPER et al. 2005, CARDINALE et al. 2006). Temporary ponds serve as important water sources for humans and their cattle in tropical savanna regions (MOHNEKE & RÖDEL 2009). Tadpoles may

play an important role in the maintenance of water quality as water quality depends on the aquatic organisms living within the respective water bodies (OSTROUMOV 2002).

I herein investigated the ecological role of tadpoles in temporary savanna ponds in West Africa and the consequences of the loss of particular tadpole species for these systems. Tadpole communities of four functionally different anuran species were combined in varying species composition in artificial ponds. Presence and absence effects of particular tadpole species on survival, growth, and development of co-occurring tadpoles were tested. To investigate the feeding ecology of the focus species and subsequently the food web ecology of these communities, the trophic position of each species needed to be determined as well as changes in trophic positions with altering community compositions. Stable isotope analyses are increasingly used to investigate food web ecology, but there are only few studies concerning stable isotope ecology of amphibian species (e.g. KUPFER et al. 2006, VERBURG et al. 2007). Furthermore, effects of altered tadpole assemblages on specific parameters of water quality, and on mosquito larvae densities and species composition were tested.

The following hypotheses were tested: (1) different tadpole species use different primary resources and hence differ in their trophic position and functional role within the food web, (2) the loss of a particular species influences trophic position, survival, growth, and development of other species within the tadpole community, (3) the loss of a particular species, and hence of a potential predator or competitor, further influences mosquito larvae densities and species occurrences, and (4) alters specific parameters of water quality in the ponds.

6.2 Materials and Methods

The experimental work was conducted at the field station of the Centre National de Gestion des Réserves de Faune (CENAGREF) in Batia, a village in the hunting and buffer zone of the Pendjari Biosphere Reserve (PBR) in northwestern Benin, West Africa (see NAGO et al. 2006 for further information on the PBR). The experiments run during the rainy seasons between July and September in 2007 and 2008.

With 32 recorded amphibian species the PBR is one of the most divers African savanna regions with regard to amphibians (NAGO et al. 2006). For this study we chose four focus species, which tadpoles differ in their feeding ecology, morphological traits and their preferred habitat, hence representing different functional groups (see appendix 4 for pictures of the four focus species). All four tadpole species are coexisting in various ponds in the PBR (own observation). Larvae of *Hoplobatrachus occipitalis* are carnivorous and prey preferentially on other tadpoles. They generally inhabit shallow water without vegetation and the pond ground. To breath atmospheric oxygen they regularly frequent the water surface. Tadpoles of *Kassina fusca* are herbivorous. They have been observed grazing on vascular plants with their massive horny beaks. They usually swim in the intermediate water column; younger stages prefer rich areas in shallower water. *Ptychadena bibroni* tadpoles are regarded to be mainly detritivorous. They feed on the pond ground and have less massive horny beaks. Larvae of *Phrynomantis microps* are filter-feeding in the upper water column. They completely lack horny beaks and keratodonts (RÖDEL 2000).

6.2.1 Species exclusion experiments

Species exclusion experiments in artificial ponds were carried out to investigate the consequences of the loss of particular tadpole species on the developmental success of other tadpole species, on water quality, and on mosquito larvae assemblages.

The experimental set up comprised 40 small plastic tanks (ST, volume: 90 l) and 38 large fiber-glass tanks (LT, volume: 200 l) as artificial ponds (Fig. 6.1). Tadpole assemblages in ST were investigated in 2007 and 2008, whereas LT assemblages were tested in 2008 only. Soil from the ground of a dried up natural savanna pond (ST: 6 l, LT: 12 l) was used as sediment to simulate natural conditions. Tanks were filled with rainwater (ST: 50 l, LT: 120 l). One meter of the common aquatic plant *Ceratophyllum submersum* was added to all LTs, as in most savanna ponds higher aquatic vegetation was present. Tanks were arranged on a plane, vegetation free area. Small tanks were covered with a net (mesh size: 2 cm) to prevent invasion and spawning by amphibians. Additionally, a fence was used in 2008 because nets alone were not efficient in keeping away frogs from the tanks in 2007. All tanks in which frogs spawned during the experiment were excluded from the analysis.

6.2.2 Collecting and raising of study species

In nights after rainfall, calling males and amplected couples of the focus species were searched at several savanna ponds and their surroundings. The single eggs of *H. occipitalis* were collected from the ponds ground in shallow water, where they are usually attached (see appendix 4). Floating egg films of *P. bibroni* were collected directly from the ponds' surfaces (see appendix 4). Amplected couples of *K. fusca* were caught and transferred to plastic basins for spawning. The spawn were transported to the research station and raised until hatching. Spawn of *P. microps* was very sensitive. In 2007 egg clutches were left in the breeding ponds and hatched larvae were captured with a dip-net some days after spawning. As it was difficult to find those young tadpoles in large numbers, spawn was carefully scooped from the water surface and transferred into plastic basins which were placed near

Figure 6.1. Set up of large and small tanks for the species exclusion experiment.

the breeding ponds in 2008. Water-level and development of larvae were regularly checked. These tadpoles were transported to the research station two days after hatching. Until the start of the experiment all tadpoles were raised with conspecifics in plastic basins filled with water from the natural breeding ponds.

6.2.3 Experimental tadpole communities

Experiments started with the tadpoles being introduced in the artificial ponds. In both size categories the following species assemblages were established: one control group in which all four species were present (ABCD, A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*), and four further treatments with one species excluded each (ABC, ABD, ACD, BCD). In ST additional treatments without the predatory tadpoles of *H. occipitalis* and one further species were set up (BC, BD, and CD). In both size categories, treatments were randomly assigned to tanks. The experiment was always conducted for a period of 14 days. In 2007 three experimental runs could be realized. In 2008 two complete experimental runs for St and LT were performed (Tab. 6.1). Data from 2007 and 2008 for ST were pooled for statistical analyses. Due to varying availability of study species, it was not possible to test all treatments in each run in equal numbers.

Table 6.1. Replication of treatments (A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*) for small (ST) and large (LT) artificial ponds for all runs in 2007 and 2008 and total sample size (n_{total}) for each treatment.

treatment	ST 2007			ST 2008		ST	LT 2008		LT
	1st run	2nd run	3rd run	1st run	2nd run	n_{total}	1st run	2nd run	n_{total}
ABCD	0	7	8	0	5	20	8	6	14
ABC	0	8	8	3	1	20	10	6	16
ABD	0	6	7	5	2	20	0	15	15
ACD	0	7	8	0	5	20	10	5	15
BCD	15	6	6	2	1	30	10	5	15
BC	7	0	0	7	6	20	-	-	-
BD	8	0	0	7	5	20	-	-	-
CD	8	0	0	0	11	19	-	-	-

Tadpoles of *H. occipitalis* are very effective predators, which are able to rapidly reduce the numbers of other tadpoles and sometimes conspecifics as well. Therefore, only one tadpole specimen of this species was introduced per tank. Densities of the other three species were chosen in relation to their predation risk (after RÖDEL 1998): in ST: *H. occipitalis* x 1, *K. fusca* x 20, *P. bibroni* x 10, *P. microps* x 50; in LT: *H. occipitalis* x 1, *K. fusca* x 20, *P. bibroni* x 20, *P. microps* x 50. As the predation risk of *P. bibroni* was higher than estimated in ST in 2007, their density was kept in St but increased in LT in 2008.

The tadpoles' age at experimental start (Tab. 6.2) was determined by time of spawning, since time of hatching could not be exactly identified for *P. microps* in 2007. Only already free swimming tadpoles were tested. All larvae were of comparable age and development stage at the start of the experiment.

Table 6.2. Range of tadpoles' age (in days after spawning) at the start of each experimental run in 2007 and 2008 for small (ST) and large (LT) artificial ponds.

Species	ST 2007			ST 2008		LT 2008	
	1st run	2nd run	3rd run	1st run	2nd run	1st run	2nd run
Hoplobatrachus occipitalis	-	2	1	2	2	1 – 2	1 – 3
Kassina fusca	11	13	12	6 – 8	10 – 14	4 – 7	6
Ptychadena bibroni	6	10	5 – 6	5 – 7	5 – 9	5 – 7	6 – 9
Phrynomantis microps	9	9 – 15	12	7 – 13	7 – 13	5 – 7	5 – 8

6.2.4 Effects of species exclusion on tadpoles' survival, growth and development

To test the influence of the community composition on each tadpole species, survival rate, growth and development stage of the larvae at the end of the experiment were compared between treatments. Therefore tanks were completely emptied through dip nets at the end of the experiment. All survived tadpoles were collected and fixed in 8% formaldehyde.

Survival time was defined as the number of tadpoles that survived the experiment in proportion to the initial number of tadpoles. To investigate the growth of tadpoles, snout-vent length (SVL) was measured and the average sizes of surviving tadpoles per tank were calculated and compared between treatments. Development stages were determined according to GOSNER (1960). Three categories of developmental stages (DS) were defined: 1^{st} category: DS 25-30, 2^{nd} category: DS 31-35, 3^{rd} category: 36-40. Average relative frequencies of developmental categories were calculated for each treatment, and absolute frequencies per treatment were compared for *H. occipitalis*.

6.2.5 Influence of tadpoles on parameters of water quality

In the artificial ponds measurements of the following water quality parameters were conducted at the start and at the end of an experiment. PH-value and electrical conductivity (EC) were measured with a Combo Tester (HI 98129 Hanna Instruments, accuracy of measurement: EC ± 2% of measuring range, pH ± 0.05). Ionic concentrations of nitrate, phosphate and ammonium were determined with colorimetric test kits (visocolor ECO, Macherey-Nagel). Water transparency (depth of visibility) was measured with a white disk attached to a measuring stick, similar to a secchi disk. Water depth was measured at five randomly chosen positions in the centre of the artificial pond and the highest value measured was taken as 100% possible depth of visibility. Measured depth of visibility was then converted to relative depth of visibility in relation to water depth. To investigate the influence of tadpoles, the differences between start- and end –values (δ pH, δ EC, δ NO_3^-, δPO_4^{3-}, δ NH_4^+) were calculated and compared between treatments. In ST ionic concentrations were only measured at the end of the experiment. In 2007 tests were performed in the third run only. Data from the end of experiment were compared between treatments.

6.2.6 Mosquito larvae composition and densities

Mosquito larvae were sampled in all artificial ponds (LT and ST) of all tadpole treatments at the experimental start (day 0), on day four, day nine, and at the end of the experiment (day 14). In order to reveal an accurate method for density determination of mosquito larvae, three different methods were applied. For the first method (dip-method) a standard mosquito dipper (volume= 350 ml), was used. Water was scooped from the surface in three consecutive dips. To ensure that larvae were disturbed as little as possible the dipper was attached onto a stick to increase the person's distance to the tank. The trapped larvae were counted, resulting in a number of larvae per three dips.

The second method (count-method) encompassed the count of all visible mosquito larvae at each of the four sample days. All mosquito larvae were counted directly in the tanks for either three minutes (ST) or five minutes (LT). While counting, it was taken care that the water was not perturbed. Fourth instar larvae which were seen when counting were preserved in 90% ethanol during only the first three samplings. For absolute numbers of mosquito larvae the 48 small and 38 large tanks were completely emptied through a plankton net (mesh width= 20 µm) at the end of the experiment. With this method all mosquito larvae in the pond were trapped (collection-method). By counting the larvae their exact number per tank was determined. All fourth instar larvae were moreover preserved in 90% ethanol and determined later on.

To assess the influences of varying tadpole combinations on mosquito larvae densities, the average numbers of counted mosquito larvae per tank and experimental run were compared between treatments for both small and large tanks. The average densities included mosquito larvae from the complete experimental period, and therefore even mosquitoes which might have emerged prior to the end of experiment (due to their short developmental time from egg to adult). All preserved larvae were identified on genus or species (when possible) level.

6.2.7 Trophic positions of tadpoles

Nitrogen and carbon stable isotopes were analysed in order to examine if intraspecific trophic position changes in dependence on community composition. Only specimens were taken from LTs in 2008. Three to fifteen individuals of all species per treatment were analysed. If possible specimens were taken from tanks in which at minimum one tadpole of each species of the tested community survived and from more than one tank per treatment. Additionally, primary consumer invertebrates (Anostraca, and snails, *Bulinus* sp.), which colonised the ponds were likewise tested. Samples were transferred from formaldehyde to 70% ethanol and stored after the field trip. Tadpoles' tail issue was prepared for isotope analyses. For removal of sediment contamination, samples were vortexed for 30 to 60 sec (Centrifuge/Vortex Combi-Spin FVL-2400). Tissue samples were than bathed and flushed with distilled water to remove residua of fixation. Samples of invertebrates were treated in the same way but the whole animal was used. All samples were dried at 40 °C for app. 48 h in a drying oven. All tadpoles and invertebrates were tested individually for their nitrogen and carbon isotope signatures. Stable isotope analysis and concentration measurements of nitrogen and carbon were performed simultaneously with a THERMO/Finnigan MAT V isotope ratio mass spectrometer, coupled to a THERMO Flash EA 1112 elemental analyzer via a THERMO/Finnigan Conflo III-interface in the stable isotope laboratory of the Museum of natural History, Berlin. Stable isotope ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$) are expressed in the conventional delta notation ($\delta^{15}N$ and $\delta^{13}C$) relative to atmospheric nitrogen and VPDB standard.

6.2.8 Statistical analyses

To compare treatments we used ANOVA, or Kruskal-Wallis tests in case that data did not show homogeneity of variances or did not follow a normal distribution. For post hoc multiple comparisons we used the Tukey test in connection with ANOVA and the Mann-Whitney test corrected for false discovery rate (fdr) subsequent to the Kruskal-Wallis tests. To test for differences between frequency distributions the Chi squared test of homogeneity was used. All statistical analyses were performed with the statistical software R (R DEVELOPMENT CORE TEAM 2009).

6.3 Results

6.3.1 Effects of species exclusion on tadpoles' survival, growth and development

6.3.1.1 *Survival rate*

No effects of species composition on the survival rate of the carnivorous *Hoplobatrachus occipitalis* tadpoles were recorded, neither in LT (X^2 test, X^2= 0.851, df= 3, p= 0.837, N= 45) nor in ST treatments (X^2 test, X^2= 0.246, df= 3, p= 0.970, N= 80). Thus, the presence or absence of a particular prey species had no influence on the survival of the predator. In LT on average 75.06% (± 5.98%) and in ST on average 81.25% (± 2.5%) of *H. occipitalis* tadpoles survived.

The survival rate of *Kassina fusca* differed significantly between treatments of varying species composition in LT (Kruskal-Wallis test, X^2= 21.897, df= 3, p< 0.001, N= 60). Significantly more larvae survived when the predatory tadpole was absent (BCD: median = 75%; post hoc Mann-Whitney test corrected for fdr; BCD vs. ABCD: p< 0.001, BCD vs. ABC: p< 0.001, BCD vs. ABD: p< 0.01, Fig. 6.2a). Between ST treatments the survival rate of *K. fusca* likewise differed between treatments of varying species composition (Kruskal-Wallis test, X^2= 64.781, df= 5, p< 0.001, N= 130). In all predator free communities (BCD: median= 62.5%, BC: median= 72.5%, BD: median= 75%) significantly more tadpoles survived than in ABCD, ABC and ABD trials. No effects of *P. bibroni* or *P. microps* could be detected in LT and ST (Fig. 6.2b).

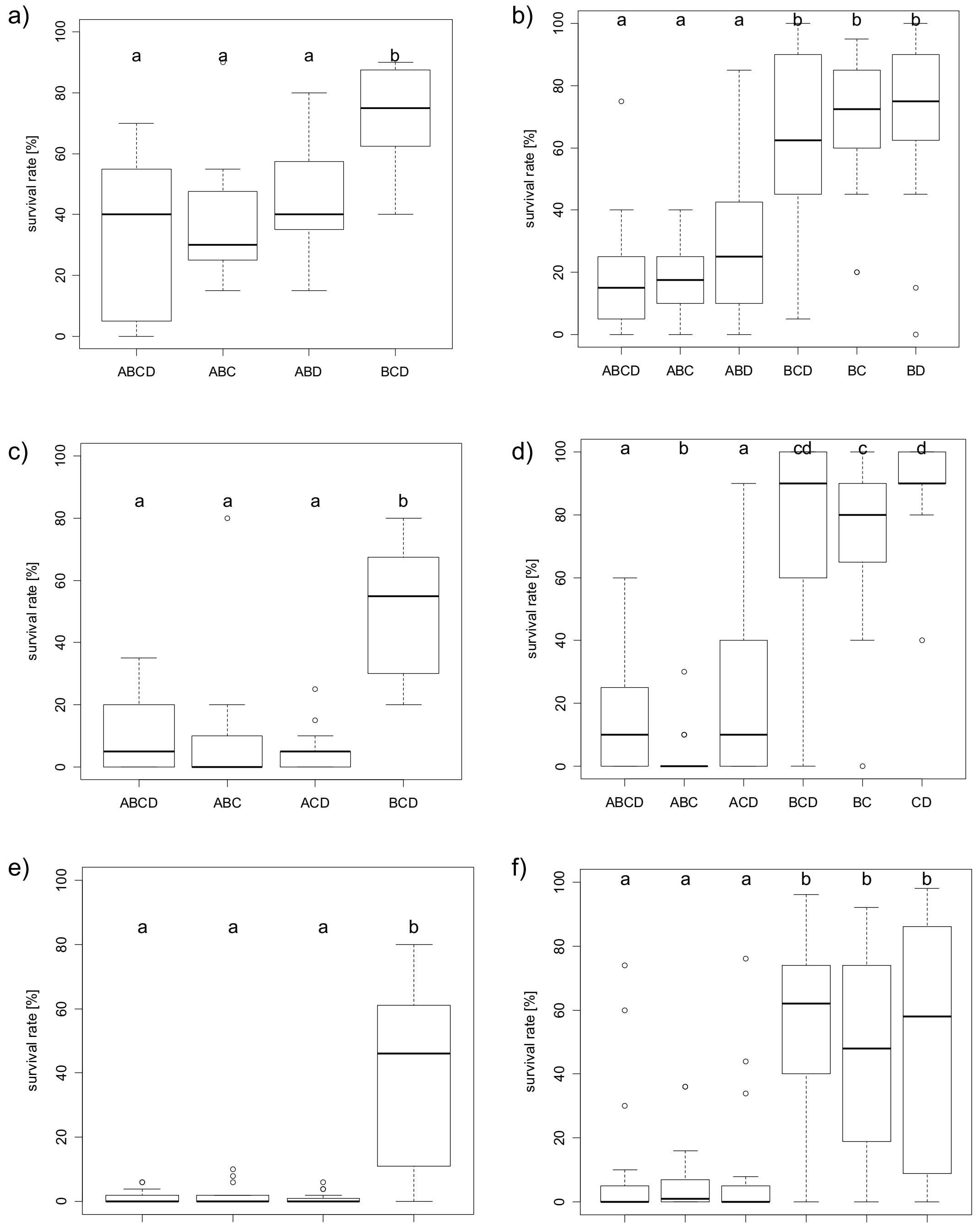


Figure 6.2. Results of post hoc multiple comparisons (Mann-Whitney test corrected for fdr) of survival rate of the respective tadpole species in treatments of varying species composition (A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*) a) Survival rate of *K. fusca* in large tanks (N= 60); b) *K. fusca* in small tanks (N= 130); c) *P. bibroni* in large tanks (N= 60); d) *P. bibroni* in small tanks (N= 129); e) *P. microps* in large tanks (N= 59) f) *P. microps* in small tanks (N= 129). Different small letters indicate significant differences between treatments.

The survival rate of *Ptychadena bibroni* also differed significantly between treatments of varying species composition in LT (Kruskal-Wallis test, X^2= 29.158, df= 3, p< 0.001, n= 60). Their survival rate was highest in BCD (median= 55%), and lowest (median= 0%) in ABC (Fig. 6.2c). There were no significant differences in survival between treatments when *H. occipitalis* was present. In ST the survival rate of *P. bibroni* differed significantly between

treatments (Kruskal-Wallis test, X^2= 76.803, df= 5, p< 0.001, N= 129). In all three predator-free communities (BCD, BC, CD) significantly more tadpoles of *P. bibroni* survived than in all three tadpole assemblages with *H. occipitalis* (ABCD, ABC, ACD) (Fig. 6.2d). The survival rate was significantly lowest, median zero, in the ST treatment in which *P. microps* was excluded (ABC). Almost all tested tadpoles died during the experiment in this community. In BC median *P. bibroni* survival was significantly lower than in CD (p< 0.01).
Survival rates of *P. microps* tadpoles significantly differed between treatments in LT (Kruskal-Wallis test, X^2= 26.076, df= 3, p< 0.001, N= 59) as well as in ST (Kruskal-Wallis test, X^2= 53.684, df= 5, p< 0.001, N= 129). In general, significantly more tadpoles survived when the larvae of *H. occipitalis* were absent (Fig. 6.2e & f). In almost all tank communities with the predator, median survival of *P. microps* was zero.

6.3.1.2 Growth

The snout-vent length of *H. occipitalis* differed significantly between treatments in LT (Kruskal-Wallis test, X^2= 18.294, df= 3, p< 0.001, N= 45). Tadpoles were significantly smallest when *P. microps* was excluded (post hoc Mann-Whitney test corrected for fdr; ABC vs. ABCD: p< 0.01, ABC vs. ABD: p= 0.03, ABC vs. ACD: p< 0.01, Fig. 6.3a & b). The same tendency was found in ST, but here no significant differences could be detected (Kruskal-Wallis test, X^2= 4.123, df= 3, p= 0.249, N= 65).
The size of *K. fusca* also differed significantly between artificial pond communities in LT (ANOVA, F= 6.25, df= 3, p= 0.001, N= 58). In median, these tadpoles were smallest in the community of ABCD (Fig. 6.3c), but significantly differed only from ABD (p= 0.002) and BCD (p= 0.005). In ST no effect of varying species composition on the growth of *K. fusca* was found (Kruskal-Wallis test, X^2= 9.295, df= 5, p= 0.098, N= 126).
Average snout-vent length of *P. bibroni* differed significantly between treatments in LT (Kruskal-Wallis test, X^2= 10.117, df= 3, p= 0.018, N= 39) as well as in ST (Kruskal-Wallis test, X^2= 19.185, df= 5, p= 0.002, N= 93). In both tank size categories median larval size was smallest in ABCD (Fig. 6.3e & f), but differed significantly only from BCD in LT (p= 0.024). In ST largest *P. bibroni* were found in CD, however, only significantly differed from ABCD (p= 0.018) and BC (p= 0.016).
The largest *P. microps* survivors in LT in median were detected in BCD, the smallest in median in the community of ABCD (Fig 6.3g). In ST larvae were largest in median in ABD and the smallest tadpoles in median were also discovered in ABCD (Fig. 6.3h). However, average snout-vent lengths did not differ significantly between treatments in LT (Kruskal-Wallis test, X^2= 1.501, df= 3, p= 0.682, N= 27) and ST (Kruskal-Wallis test, X^2= 5.368, df= 5, p= 0.373, N= 87).

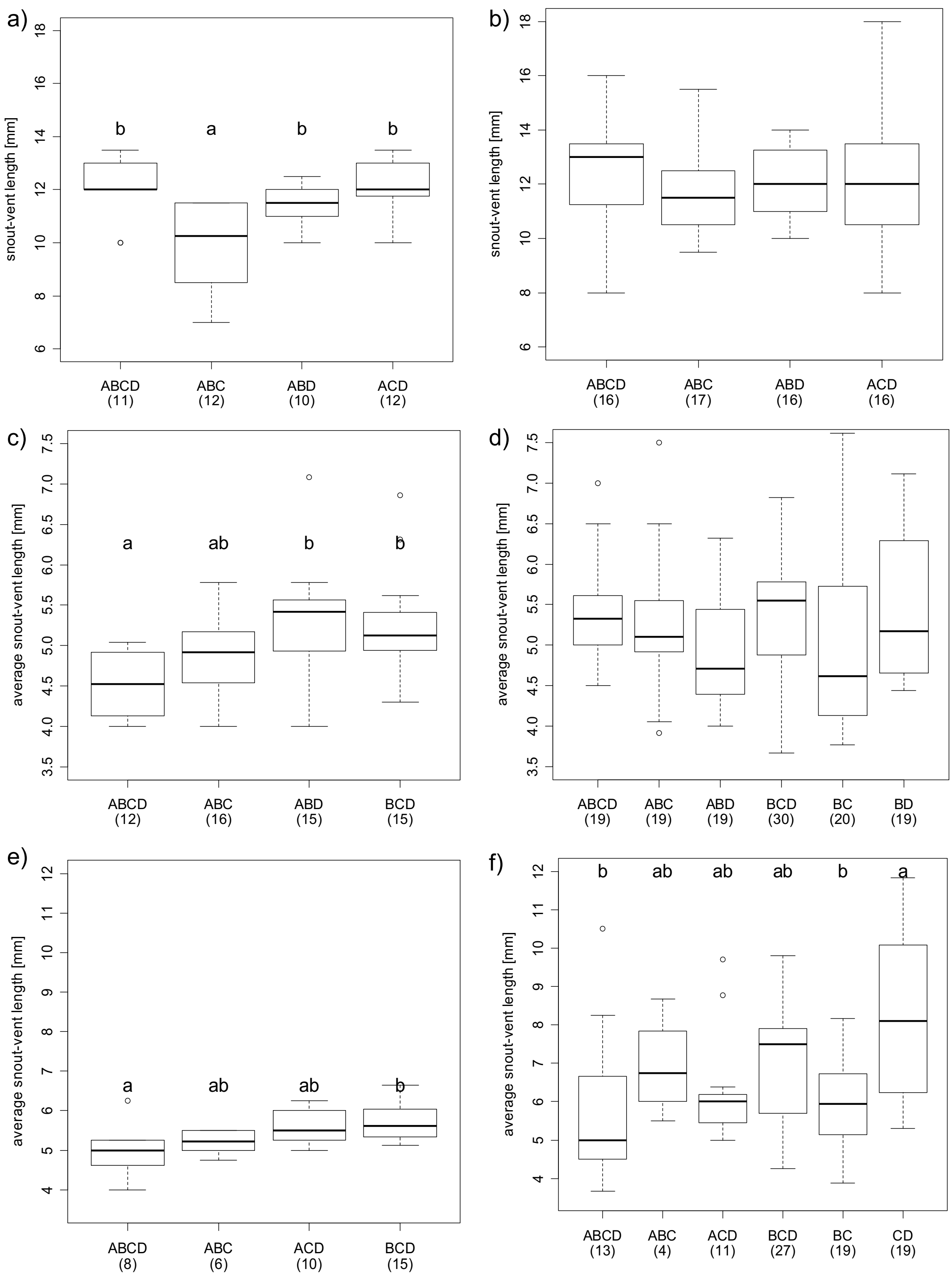


Figure 6.3. Results of post hoc multiple comparisons (Mann-Whitney test corrected for fdr) of average snout-vent length of the respective tadpole species in treatments of varying species composition (A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*) a) *H. occidentalis* in large tanks; b) *H. occidentalis* in small tanks; c) *K. fusca* in large tanks; d) *K. fusca* in small tanks; e) *P. bibroni* in large tanks; f) *P. bibroni* in small tanks, g) *P. microps* in large tanks (next page), h) *P. microps* in small tanks (next page). Sample size per treatment (number of tanks in which individuals survived) is given in brackets. Different small letters indicate significant differences between treatments.

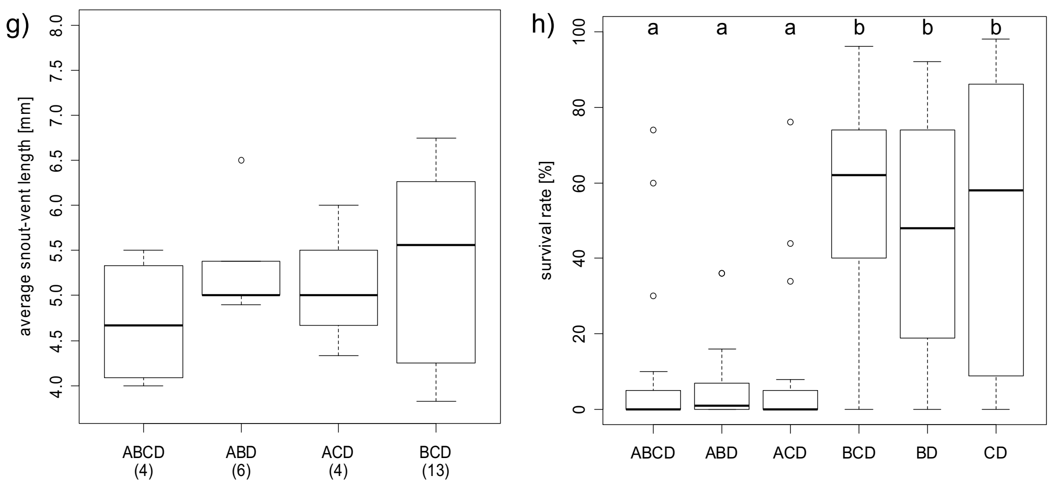


Fig. 6.3. continued

Generally, data were based on very few individuals of *P. bibroni* and especially *P. microps* in treatments in which the carnivorous tadpoles of *H. occipitalis* were present, as in most cases these species did not survive the experiment in those communities.

6.3.1.3 Development

In LT treatments larvae of *H. occipitalis* developed only to developmental categories one and two. The frequency of developmental categories differed significantly between treatments (X^2 test, X^2= 23.377, df= 3, p< 0.001, N= 45). In ABCD and in ACD more than 80% of these tadpoles reached category two. In ABD only 30% developed into category two. In the treatment without *P. microps* (ABC) all larvae of *H. occipitalis* remained in category one. In ST treatments *H. occipitalis* tadpoles finished the experiment in all three developmental categories. In ABCD as well as in ACD some *H. occipitalis* developed to category three. In both other communities' only category one and two were reached. However, these differences were not significant (X^2 test, X^2= 11.734, df= 6, p= 0.068, N= 65).

Tadpoles of *K. fusca* only reached developmental category one in all treatments in LT and in ST. *P. bibroni* larvae also were found in category one only in all treatments of the LT. In the ST CD treatment on average 63.9% of *P. bibroni* remained in category one, 25.5% developed into category two, and 10.58% developed into category three. In all the other treatments only category one *P. bibroni* tadpoles were recorded at the end of experiments.

In LT larvae of *P. microps* remained in category one in most treatments. Just in the community without *H. occipitalis*, on average 0.7% reached developmental stage two. In ST larvae were merely found in category one in the community of ACD, BD and CD. In the other communities (ABCD, ABD, BCD), some larvae in more advanced stages were detected.

6.3.2 Tadpoles' trophic position in relation to community composition

The tested tadpole species varied in their trophic positions as $\delta^{15}N$ significantly differed between tadpole species in the control treatment ABCD (ANOVA, $F = 13.107$, $df = 3$, $p < 0.001$, $n = 36$). As suspected, the predatory *Hoplobatrachus occipitalis* had significantly higher $\delta^{15}N$ ratios than *Kassina fusca* (Tukey test, $p < 0.001$) and *Phrynomantis microps* ($p = 0.002$). However, $\delta^{15}N$ of *Ptychadena bibroni* was only slightly lower than in *H. occipitalis* (Tab. 6.3, $p = 0.832$), and significantly higher than in *K. fusca* ($p < 0.001$) and *P. microps* ($p = 0.004$). No differences in $\delta^{15}N$ between *K. fusca* and *P. microps* were found ($p = 0.993$). The four tadpole species had no differences in their $\delta^{13}C$ signatures in the control treatment (ANOVA, $F = 1.1455$, $df = 3$, $p = 0.3457$). The isotope analyses confirmed *H. occipitalis* to be a top predator with highest $\delta^{15}N$ in all LT treatments (Tab. 6.3). The average enrichment in $\delta^{15}N$ of all tested *H. occipitalis* (average $\delta^{15}N = 6.96‰ \pm 1.11$, $n = 15$) in relation to the three prey tadpole species (average $\delta^{15}N = 5.20‰ \pm 1.07$, $n = 118$) was 1.77‰. The difference in $\delta^{13}C$ of *H. occipitalis* (average $\delta^{13}C = -20‰ \pm 0.9$, $n = 15$) and the other three tadpole species (average $\delta^{13}C = -20.83‰ \pm 1.28$, $n = 118$) was 0.83‰.

We then compared intraspecific nitrogen and carbon isotope signatures of the different species, kept in different LT treatments to reveal potential changes in trophic position with regard to community composition (Tab. 6.3). Trophic position of *H. occipitalis* tadpoles did not change with species composition. Neither their $\delta^{15}N$ signatures (ANOVA, $F = 2.6935$, $df = 3$, $p = 0.0974$, $n = 15$), nor their $\delta^{13}C$ signatures (ANOVA, $F = 0.0877$, $p = 0.9653$, $n = 15$) differed between treatments.

In contrast *K. fusca* tadpoles showed variations in their nitrogen isotope signatures depending on community composition (Kruskal-Wallis test, $\chi^2 = 19.5516$, $df = 3$, $p < 0.001$, $n = 56$). In the treatment without *H. occipitalis* $\delta^{15}N$ ratios were significantly higher than in all other communities (post hoc Mann-Whitney test corrected for fdr; BCD vs. ABCD: $p < 0.001$; BCD vs. ABC: $p = 0.001$; BCD vs. ABD: $p = 0.014$; Tab. 6.3). No differences in $\delta^{13}C$ were found between treatments (Kruskal-Wallis test, $X^2 = 6.9331$, $df = 3$, $p = 0.074$, $n = 56$).

In *P. bibroni* differences in $\delta^{15}N$ ratios (ANOVA, $F = 3.5084$, $df = 3$, $p = 0.0252$, $n = 39$), as well as in $\delta^{13}C$ ratios (Kruskal-Wallis test, $\chi^2 = 15.8174$, $df = 3$, $p < 0.01$, $n = 39$) occurred between treatments. Their $\delta^{15}N$ ratios were lower in the treatment in which *K. fusca* was excluded. Significant differences were found between the ACD and ABC communities ($p = 0.046$), and between the ACD and BCD communities ($p = 0.014$). Their $\delta^{13}C$ ratios were significantly more depleted in the treatment without *H. occipitalis* than in all other communities (BCD vs. ABCD: $p = 0.002$; BCD vs. ABC: $p = 0.022$; BCD vs. ACD: $p = 0.022$).

Tadpoles of *P. microps* showed no significant differences in $\delta^{15}N$ ratios between treatments (ANOVA, $F = 1.9386$, $df = 3$, $p = 0.2367$, $n = 23$). However, their $\delta^{13}C$ ratios significantly differed between treatments (Kruskal-Wallis test, χ^2 = 11.8152, df = 3, p < 0.01, n = 23). In BCD $\delta^{13}C$ was significantly more depleted than in ACD (p = 0.033).

Table 6.3. Average nitrogen and carbon stable isotope signatures (± 1 SD) and sample size (N) of tested tadpoles per treatment of varying species composition (A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*) and tested invertebrates in artificial ponds of the species exclusion experiment.

Species / organism	treatment	N	$\delta^{15}N$ [‰]	$\delta^{13}C$ [‰]
(A) Hoplobatrachus occipitalis	ABCD	6	6.13 ± 0.79	-20.14 ± 0.85
	ABC	3	7.71 ± 1.55	-19.90 ± 0.69
	ABD	3	7.25 ± 0.34	-19.98 ± 1.63
	ACD	3	7.59 ± 0.95	-19.81 ± 0.76
(B) Kassina fusca	ABCD	15	4.46 ± 0.66	-20.78 ± 1.05
	ABC	13	4.39 ± 1.15	-20.63 ± 1.95
	ABD	13	4.82 ± 1.12	-20.41 ± 1.03
	BCD	15	6.07 ± 0.65	-19.79 ± 1.04
(C) Ptychadena bibroni	ABCD	10	5.81 ± 0.80	-20.10 ± 1.11
	ABC	11	5.90 ± 0.77	-20.75 ± 1.21
	ACD	3	4.38 ± 0.31	-20.67 ± 0.53
	BCD	15	6.13 ± 0.99	-21.70 ± 0.37
(D) Phrynomantis microps	ABCD	5	4.36 ± 0.64	-20.68 ± 1.03
	ABD	4	4.46 ± 0.77	-22.72 ± 0.82
	ACD	3	4.54 ± 0.34	-20.39 ± 0.43
	BCD	11	4.91 ± 0.23	-22.10 ± 0.29
Anostraca		15	2.02 ± 1.33	-26.34 ± 1.03
Gastropoda		5	3.36 ± 1.40	-20.41 ± 1.40

6.3.3 Influence of tadpoles on water chemistry and transparency

In LT artificial ponds pH-values ranged from 4.47 to 7.88 at the start of experiments and between 7.18 and 7.99 at their end. The very low value of 4.47 is just one outlier. In ST pH-values were between 5.96 and 8.25 at the start, and between 6.25 and 8.91 at the end of the experiment. The pH-values changed slightly in most artificial ponds during the experimental period; in some pH increased, in others it decreased. The differences in pH between the start and the end of the experiment (δ pH) differed significantly between treatments in LT (Kruskal-Wallis test, X^2= 21.372, df= 4, p< 0.001, N= 75) and ST (Kruskal-Wallis test, X^2= 39.384, df= 7, p< 0.001, N= 169).

In both pond size categories no clear pattern of the dependency of δ pH on the presence or absence of *H. occipitalis*, *K. fusca*, *P. bibroni* or *P. microps* tadpoles was found (see Fig. 6.4).

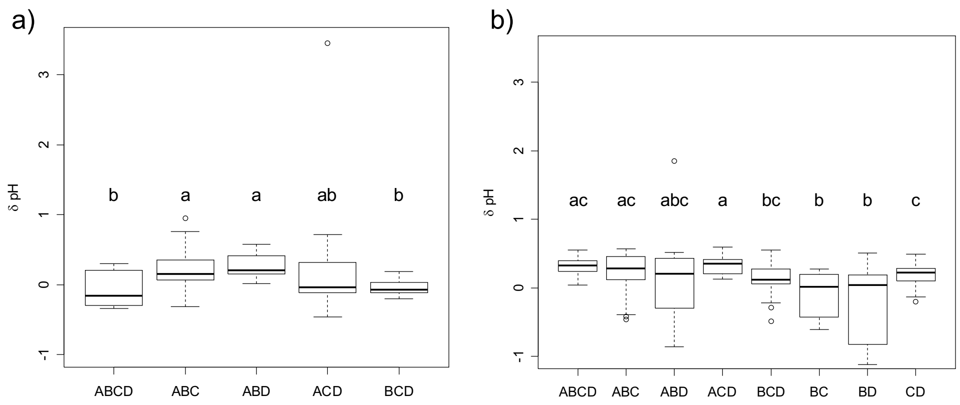


Figure 6.4. Results for post hoc multiple comparisons (Mann-Whitney test corrected for fdr) for differences in pH (δ pH) between the start and end of the experiment in treatments of varying species composition (A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*) in a) large tanks (N= 75) and b) small tanks (N= 169). Different small letters indicate significant differences between treatments.

Conductivity (EC) was between 0 and 18 µS/cm at the start as well as at the end of the experiment in large artificial ponds. In the small artificial ponds it ranged between 1 and 108 µS/cm (median= 9 µS/cm) at the beginning, and between 1 and 88 µS/cm (median= 12 µS/cm) at the end of experiments. The high values of 108 µS/cm at the start and 88 µS/cm at the end of the experiment were outliers measured in the same tank. In LT EC was in the lower range of EC in natural ponds in some tanks, but even lower in others (see Riemann 2010). With the above mentioned exception, the same pattern was found in ST. The differences in EC between the start and the end of the experiment (δ EC) differed significantly between treatments in LT (Kruskal-Wallis test, X^2= 26.666, df=4, p< 0.001, N= 75). In ABCD and ABC EC decreased during experimental time, whereas EC in median increased in ABD (Fig. 6.5). In ACD and BCD in median EC did not change. In ST, EC did not change in median during experimental time in some communities, in others it increased in median, and only in BC the electric conductivity in median decreased. However, no significant differences between treatments were found for changes in EC between start and end of the experiment in ST (Kruskal-Wallis test, X^2= 12.825, df= 7, p= 0.077, N= 169).

Measured concentrations of nitrate varied between 0 and 10 mg/l at the start and between 0 and 5 mg/l at the end of the experiment in LT. In ST concentrations between 0 and 3 mg/l were detected at the end of experimental time. Nitrate concentrations in ST were within the same range of nitrate concentrations in natural ponds. In some large tanks, higher concentrations than in natural ponds were detected.

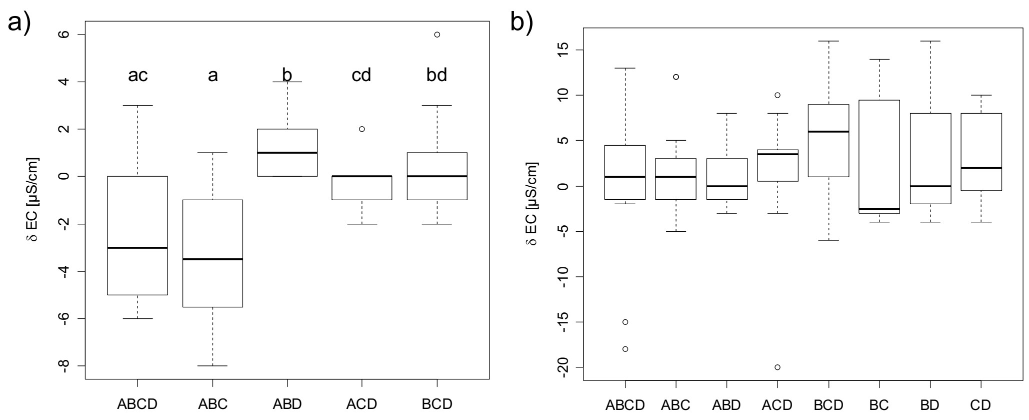


Figure 6.5. Results for post hoc multiple comparisons (Mann-Whitney test corrected for fdr) for differences in electrical conductivity (δ EC) between the start and end of the experiment in treatments of varying species composition (A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*) in a) large tanks (N= 75) and b) small tanks (N= 169). Different small letters indicate significant differences between treatments.

In LT nitrate concentrations did not change in median in ABC as well as in ABD, but slightly decreased in median in the other treatments (Fig. 6.6). Though, the differences of nitrate concentrations (δ NO_3^-) between the start and the end of the experiment did not differ significantly between treatments (Kruskal-Wallis test, X^2= 5.648, df= 4, p= 0.227, N= 75).

Phosphate was measured in concentrations between 0 and 5 mg/l at the start, and between 0 and 3 mg/l at the end of the experiment in LT. Concentrations lay between 0 and 0,7 mg/l at the end of the experiment in ST. Here, phosphate concentrations were within the same range of concentrations in natural ponds. In LT, partly higher concentrations than in natural ponds were measured.

The differences in phosphate concentrations between the start and the end of the experiment (δ PO_4^{3-}) differed significantly between treatments in LT (Kruskal-Wallis test, X^2= 19.375, df= 4, p< 0.001, N= 75). In ACD phosphate concentration in median decreased by 1.3 mg/l during the experimental time and differed significantly from all other treatments (Fig. 6.6). In those it did not change in median or decreased marginally in median (-0.1).

Concentrations of ammonium were between 0 and 0.4 mg/l at the start and between 0 and 0.25 mg/l at the end of experimental time in LT. In ST concentrations between 0 and 2 mg/l were detected. In both pond sizes, ammonium concentrations were within the same range of ammonium concentrations in natural ponds (second investigation). In LT ammonium concentrations did not change in median during the experimental time in all communities of varying species composition. Thus, the differences of ammonium concentrations (δ NH_4^+) between the start and the end of the experiment did not differ significantly between treatments (Kruskal-Wallis test, X^2= 3.026, df= 4, p= 0.554, N= 75).

The relative depth of visibility differed significantly between the communities of varying species compositions in LT at the end of the experiment (Kruskal-Wallis test, X^2= 9.944, df= 4, $p < 0.05$, N= 75), but post hoc multiple comparisons (Mann-Whitney test corrected for fdr)

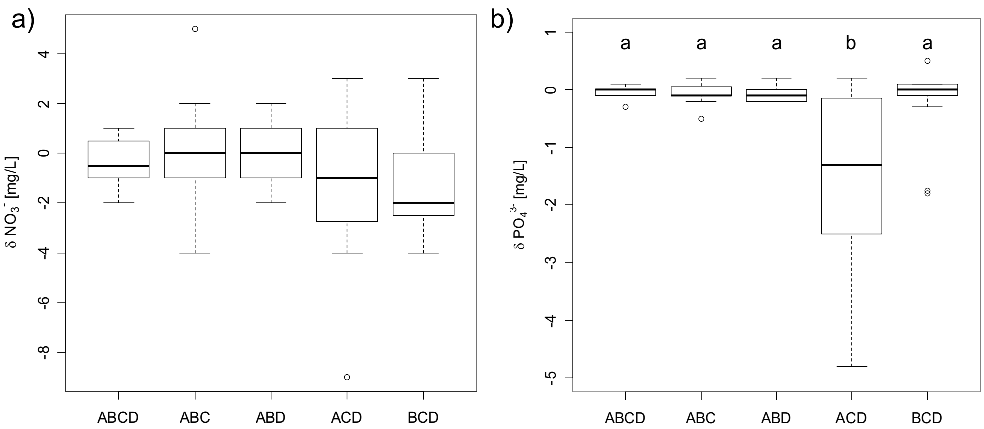


Figure 6.6. Differences in a) nitrate concentrations (δ NO_3^-) and in b) phosphate concentrations (δ PO_4^{3-}) between the start and end of the experiment in treatments with varying species composition (A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*) in large tanks. Different small letters indicate significant differences between treatments (N= 75 for both a) and b)).

did not reveal significant differences between any treatments. Relative depth of visibility was highest in BCD (median= 65%), followed by ABCD (median= 63.43%). Lowest relative depth of visibility was detected in ABC, where the filter feeding *P. microps* larvae were excluded (median= 27.9%). In both other communities depth of visibility was around 40% (Fig. 6.7). In ST, relative depth of visibility also differed significantly between treatments at the end of experimental time (Kruskal-Wallis test, X^2= 54.439, df= 7, $p < 0.001$, N= 169). Relative depth of visibility was in median 100% in all predator free communities in which *P. microps* tadpoles were present (Fig. 6.7). These treatments differed significantly from communities in which larvae of *P. microps* were excluded, and from those treatments where *P. microps* tadpoles did not survive the experimental time because *H. occipitalis* was present (Fig. 6.7).

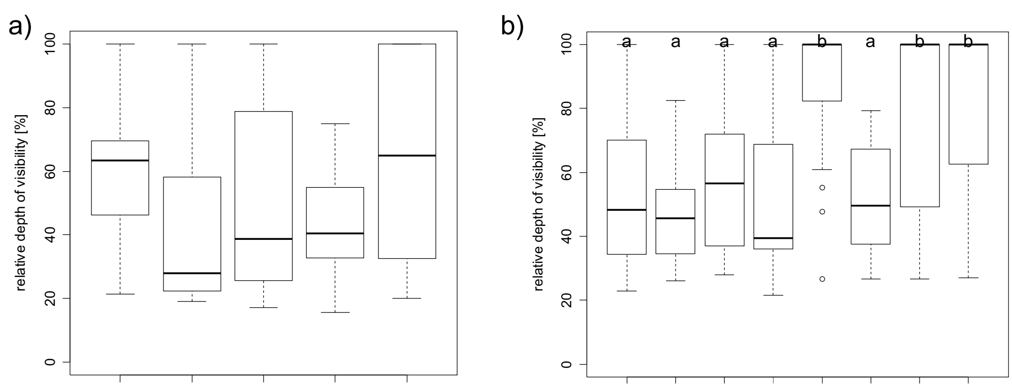


Figure 6.7. Relative depth of visibility measured at the end of experimental time in the treatments of varying species composition (A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*) in a) large tanks (N= 75) and b) small tanks (N= 169). Different small letters indicate significant differences between treatments.

6.3.4 Mosquito assemblages and densities

Regarding the small tanks (N= 135), all collected mosquito larvae either belonged to the genus *Anopheles* (42% out of 814 individuals), *Aedes* (41%), or *Culex* (17%). Besides, one single individual of *Lutzia tigripes* was found. Among the collected larvae of the genus *Anopheles*, almost all individuals (96%) belonged to the species complex *Anopheles gambiae* s.l., the remaining 4% being *Anopheles rufipes*. All identified *Culex* larvae were *Culex inconspicuosus,* and all individuals of the genus *Aedes* belonged to the species *Aedes vittatus*.

The mosquito larvae recorded in the large tanks (N= 75) were predominantly of the genus *Anopheles* (88%, 331 out of 376 individuals) followed by *Culex* (10%) and a small number of *Aedes* (2%). Among those individuals, larvae that could be determined on species level belonged to *Anopheles gambiae* s.l., *Culex inconspicuosus*, and *Aedes metallicus*.

However, I found no evidence for my assumptions that mosquito larvae numbers are lower in the presence of predatory tadpoles (*H. occipitalis*) and in the presence of competitors (*Kassina fusca*, *Phrynomantis microps*, and *Ptychadena bibroni*) (Fig. 6.8). No significant differences in the average number of mosquito larvae were found between the different treatments in ST (Kruskal-Wallis-test, X^2= 71.77, df= 68, p= 0.35, N= 135) and also not in LT (Kruskal-Wallis test, X^2= 48.91, df= 41, p= 0.19, N= 75). Thus, the presence or absence of any tadpole species did not influence densities of mosquito larvae.

However, there were differences of mosquito larval abundances between artificial ponds, but these differences were independent of tadpole compositions. Therefore, other factors, such as abiotic parameters, might have been responsible for differences in mosquito larvae densities between ponds.

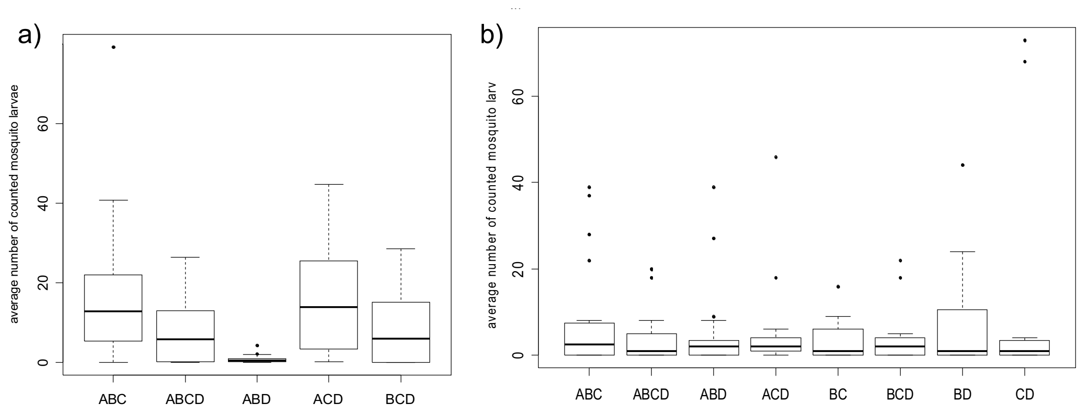


Figure 6.8. Average number of counted mosquito larvae in the treatments of varying species composition (A: *H. occipitalis*, B: *K. fusca*, C: *P. bibroni*, D: *P. microps*) in a) large ponds (N= 75) and in b) small ponds (N= 135).

6.4 Discussion

Various studies have already demonstrated that amphibians play important roles in their respective ecosystems (reviewed in WHILES et al. 2006). With the results of these species exclusion experiments I am able to contribute to the understanding in how ecosystems may be affected through the loss of amphibian species, particularly with regard to tropical savanna habitat. The species exclusion experiment revealed various differences in survival, growth, development and feeding activity of all four focus species depending on assemblage composition.

Hoplobatrachus occipitalis has been shown to be an important top predator with profound impact on the population structure of the prey species. These tadpoles clearly influenced the survival rates of the other three tadpole species in a crucial way by severely reducing their numbers in each community combination. In LT as well as ST treatments significantly more larvae of all three prey species survived the experiment in the absence of *H. occipitalis*. In all larval stages, *H. occipitalis* is a very effective predator, which is able to substantially minimize other tadpole's densities (RÖDEL 1998). For example, in a small temporary savanna pond with a water volume of 220 l, hence directly comparable with the tanks used in the experiment, 74 recently hatched *H. occipitalis* larvae devoured all hatchlings of a *Bufo maculatus* clutch (minimum of 2000 tadpoles) within three days (RÖDEL 2000).

The survival rates were highest for *Kassina fusca* and lowest for *Phrynomantis microps* in the presence of the predator. In general, population densities can be regulated at the larval and adult stage in amphibians, but often high mortality during the larval stage is of greater importance (reviewed in WILBUR 1980). Extremely low rates of metamorphosis were found in all three tested prey species, and are generally common in West African savanna anurans (RÖDEL 1998), indicating that regulation of population densities occurs during the larval stage. This might be of particular importance for *P. microps*, as adults are poisonous (RÖDEL 1998) and thus probably protected against various potential predators. Therefore, *H. occipitalis* might play an important role in structuring the population densities of *P. microps*, and of other prey species as well.

Predation causes mortality and costs of induced defence in the prey populations, but can also have a positive effect by reducing intra- and interspecific competition (WILBUR 1987, 1997). In this study, prey populations were under a strong top-down control of the predatory tadpoles. BEARD et al. (2003) reported top-down control effects of adult frogs on herbivorous prey dynamics and indirect positive effects on plant performance in a tropical rainforest. This might also count for an aquatic larval predator. By controlling the numbers of herbivorous tadpoles, *H. occipitalis* may allow higher phytoplankton and periphyton growth rates and in this way providing enough food for surviving tadpoles, which would resemble a typical trophic cascade (PACE et al. 1999). Thus, an eradication of *H. occipitalis* could lead to an increase in

intra- and interspecific competition of prey species, due to a decrease in food availability with increasing tadpole densities. There is evidence from various studies that high intra- and/or interspecific densities negatively effect growth rates, lead to a prolongation of developmental time, and cause reduced sizes at metamorphosis of anuran larvae (e.g. WILBUR 1987, FLECKER et al. 1999, LOMAN 2001, 2004, RUDOLF & RÖDEL 2005). Reduced size at metamorphosis in turn negatively affects fecundity and reproductive success of adult anurans (reviewed in WILBUR 1997). Hence, the loss of *H. occipitalis* might have fatal consequences for the population structures of various prey species with possible cascading extinctions (THÉBAULT et al. 2007). This is of particular importance in regard of the possible threat to *H. occipitalis* due to overexploitation (see chapter 3).
Furthermore, survival rates of *Ptychadena bibroni* were in tendency lowest when tadpoles of *P. microps* were absent in LT and was significantly worst in ST. These findings indicate that the presence of *P. microps* had an indirect beneficial effect on the survival of these tadpoles. Therefore, if the susceptibility to predation of *P. microps* compared to other species is also higher under natural conditions, the loss of *P. microps* could lead to a higher predation pressure on tadpoles of other anuran species in general. If a species is not able to adapt quickly to such a situation, crucial consequences for their population structures are possible. But direct beneficial effects are also possible. By altering resources through their feeding behaviour, *P. microps* tadpoles could provide essential nutrients for the larvae of *P. bibroni*, or nutrients needed by a resource which was exploited by *P. bibroni.* Due to their filter-feeding activity, *P. microps* larvae may partly ingest various particles from the water column which they do not assimilate (ALTIG et al. 2007). However, those materials could be processed during intestine passage and bound in the tadpoles' faeces and would thus be made available for the benthic detrital food web (OSTROUMOV 2005).

One major finding of the experiment was that changes in intra-specific isotope signatures in some species were related to species exclusion. Hence, food web functioning can change depending on the presence and absence of particular tadpole species. The detected differences in trophic positions and functions of the four focus species further let to different ecological roles of the tadpoles in the ponds.
Surprisingly, we could not detect significant differences in $\delta^{15}N$ signatures between *H. occipitalis* and *P. bibroni* and between *K. fusca* and *P. microps* tadpoles. Although we would have assumed *P. bibroni* tadpoles to be detritivorous, they had the highest $\delta^{15}N$ signatures within the prey tadpole species. There is evidence from natural ponds that they feed on terrestrial detrital plant material or microbes and subsequently show relative low $\delta^{15}N$ signatures in comparison to tadpoles of other trophic levels (RIEMANN 2010). These resources were probably not available in the artificial ponds. In natural ponds terrestrial plant

material is probably mainly flushed into ponds from the surroundings during heavy rainfalls. Concerning the artificial ponds, terrestrial plant material could only enter the ponds through the air since the tanks were not at ground level. Thus, the time interval of the artificial ponds duration might have been too short for detritus material to accumulate. Hence, larvae of *P. bibroni* might have fed on autochthonous detritus or related microbes in the experiment, whereas in natural ponds they might feed rather on allochthonous material. They might have even fed on remaining parts of dead tadpoles (PETRANKA & KENNEDY 1999), which were left over by *H. occipitalis* tadpoles in the experiment, which may explain their similar $\delta^{15}N$ signatures. A limited resource supply could likewise be the reason for the similar $\delta^{15}N$ signatures of *K. fusca* and *P. microps*. It is known that rasping tadpoles can suspension feed under specific circumstances (in ALTIG 2010). Thus, a limited supply of aquatic plants could have led to a suspension feeding behaviour by *K. fusca* to some extent. In case they have used different resources, those resources could, however, have had similar isotope signatures (VERBURG et al. 2007). We would assume that they have different feeding behaviours, due to morphological differences of their oral and buccopharyngal structures (ALTIG et al. 2007, STRAUß et al. 2010) and there is further evidence that they indeed differ in $\delta^{15}N$ signatures in natural ponds (RIEMANN 2010). Hence, alteration in tadpoles' feeding behaviour may be possible under altered environmental conditions and under limited resource supply in particular. This finding is in accordance with SCHIESARI et al. (2009) who reported opportunistic feeding habits and shifts in diet by tadpoles of four ranid species (*Lithobates sylvaticus*, *L. pipiens*, *L. clamitans*, *L. catesbeianus*).

The mean trophic enrichment in $\delta^{15}N$ of *H. occipitalis* in relation to the prey tadpoles was only 1.76‰, which seems to be very low compared to the average $\delta^{15}N$ enrichment of 3.4‰ per trophic level reported in the literature (VANDER ZANDEN & RASMUSSEN 2001, POST 2002). A similar $\delta^{15}N$ fractionation (1.98‰) was reported by SCHIESARI et al. (2009) for tadpoles of wood, leopard and green frogs, which implied their trophic position as primary predators. They mainly found evidence that these tadpole species feed on invertebrates. There is evidence that *H. occipitalis* also fed on invertebrates such as mosquito larvae (NOPPER 2010). However, mosquito larvae were not included in the isotopic analysis. Also Anostraca, which had lowest $\delta^{15}N$ signatures in the experiment, are potential prey. These potential preys should have been integrated in the calculation of trophic fractionation because the enrichment in $\delta^{15}N$ due to an invertebrate diet is lower than enrichment due to a vertebrate diet (MCCUTCHAN et al. 2003).

The larvae of *K. fusca* had significantly higher $\delta^{15}N$ signatures in the community in which the predatory *H. occipitalis* tadpoles were excluded. This indicates a shift in their trophic position and used resources. As their $\delta^{13}C$ signatures did not change in this community they seemed to switch to a more omnivorous diet. Interestingly, no effects of the presence of the predator could be detected on growth and development of *K. fusca*, but obviously predation affected their feeding behaviour. The exclusion of *K. fusca* led to a significant decrease in phosphate concentrations. Since the growth of primary producers is generally limited by phosphorous (BRÖNMARK & HANSSON 2005), a higher uptake of phosphate points to an increase in primary production. Hence, the herbivorous *K. fusca* tadpoles might have reduced primary production in all treatments in which they were present.

Tadpoles of *P. bibroni* changed their trophic position in the treatment without *K. fusca* towards a similar $\delta^{15}N$ as *K. fusca*. This result supports the assumption from the investigation of development that *K. fusca* might have competitive effects on *P. bibroni*. As resources seemed to be rather limited in artificial ponds in comparison to natural ponds, distinct competitive effects were likely. The predator may also have affected the feeding behaviour of *P. bibroni* as their $\delta^{13}C$ in the community without *H. occipitalis* significantly differed from other treatments. However, the detected differences in $\delta^{13}C$ were very small and most likely did not reflect different primary resources. It might hence be doubtful that these differences are of any biological relevance. Likewise, significant differences in $\delta^{13}C$ of *P. microps* between the community without *H. occipitalis* and the treatment without *K. fusca* did not reflect different primary resources and hence were of no biological relevance.

Generally, information on feeding behaviours is central to understand the ecological roles of tadpoles because feeding behaviour is often linked to functional roles (e.g. altering resource availability or quality for other consumers) and can result in both positive and negative interactions with other consumers (ALTIG 2007). Herein we could show that tadpoles are able to change their feeding behaviour. ALTIG et al. (2007) proposed that a change in tadpoles' diet could be due to its spatiotemporal variation. The similarity of nitrogen istotope signatures in some species (in *H. occipitalis* and *P. bibroni*, and in *K. fusca* and *P. microps*) was probably due to the limited resource availability in the experimental tanks in comparison to natural ponds, which supports this assumption. The detected changes of isoptope signatures within tadpole species, particularly in *K. fusca* and *P. bibroni*, during the experiment were further dependant on the community composition. In scope of alterations in amphibian communities due to disturbance events such changes in tadpoles' feeding ecology are thus likely to happen in natural ecosystems. Tadpoles are supposed to act as ecosystem engineers in many systems by modifying certain habitat parameters and/or other consumers (KUPFERBERG 1997, FLECKER 1999, RANVESTEL et al. 2004, WHILES et al. 2006). Hence, an altered tadpole community with subsequent altered feeding behaviours of the individuals could even lead to changes in ecosystem functions. In the following possible effects of altered tadpole communities on water parameters and on co-occurring mosquito larvae are reconsidered.

6.4.1 Tadpoles' effect on water transparency and water chemistry

We detected a strong positive effect of the filter feeding *P. microps* tadpoles on water transparency, since depth of visibility was significantly higher in presence of *P. microps* in ST. In communities with the predator no effects were found because the vast majority of *P. microps* tadpoles did not often survive in these treatments. The transparency effect was weaker in LT, indicating that the filtering capacity is density dependent.
Phrynomantis microps tadpoles were obviously responsible for higher water transparency due to their filter-feeding activity. Filter feeding tadpoles are able to ingest particles between 0.126 µm (WASSERSUG 1972) and 200 µm (SEALE 1980). The filtering activity of many filter feeders is so profound, that the whole water volume of a given water body is filtered within some days (OSTROUMOV 2005). VIERTEL (1992) reported a maximum filter feeding capacity of 850 ml filtered water per 30 minutes per gram for tadpoles of *Xenopus laevis* (at stage 28 according to GOSNER 1960). Filter feeders provide various ecosystem services and make an important contribution to the "ecological repair of water quality" (OSTROUMOV 2005). A decline in filter feeding tadpoles, especially in obligate filter feeders, might have crucial consequences for the ecosystem and can result in eutrophication of ponds (SEALE 1980, OFFICER et al. 1982). That would especially come hard for the humans in tropical savanna regions, as temporary waters are essential for local populations and their cattle (see Chapter 2), but also wildlife may be negatively affected.
Concerning the other parameters of water chemistry, we found no influence of the tested tadpole species on pH, EC, nitrate and ammonium concentrations. Either no influences of species composition on these parameters were detected or revealed differences could not be explained by the presence or absence of particular tadpole species. Maybe those suspected indirect effects of tadpoles on these water quality parameters were too low to be detected. Maybe also experimental time was not sufficient for the establishment of a profound algal community and thus the ability of the tadpoles' impact was limited. Perhaps, tadpole densities were not large enough to substantially affect those parameters. Possible effects of *P. bibroni* and *P. microps* might have been not discoverable because these species generally did not survive in presence of *H. occipitalis*.

6.4.2 Mosquito densities and species assemblages in respect to tadpole species exclusion

Although mosquito larvae differ in their ways of feeding, species specific information is lacking. *Anopheles* and *Culex* larvae are filter feeders. Whereas *Anopheles* larvae forage in the surface layer of ponds, larvae of *Culex* forage in the mid water column (MERRIT et al. 1992). *Aedes* larvae are browsers feeding mostly on loosely attached microorganisms and detritus on surfaces below water. Adult mosquitoes of *Aedes* usually lay their eggs on substrate above water line, which is flooded after rain events (BENTLEY & DAY 1989). *Lutzia tigripes* larvae are carnivorous and feed on other mosquito larvae as well as small invertebrates (HOPKINS 1952, own observations). Hence, mosquito communities comprised of mosquito larvae belonging into four different feeding groups. It is therefore likely, that tadpoles and mosquito larvae were occupying similar trophic positions and might have competed over the same nutritional resources. Among the focus species, *Kassina fusca*, *Ptychadena bibroni*, and *Phrynomantis microps* were hypothesised to compete with mosquito larvae over resources and to indirectly affect their larval densities. Such an interaction was found for tadpoles of *Lymnodynastes peronii,* which reduced the survival of mosquito larvae of *Culex quinquefasciatus* (MOKANY & SHINE 2003a).

However, no effects of the presence and/or absence of tadpole species on mosquito larvae densities and assemblage composition were found including no effect of competitive interaction between tadpoles and mosquito larva. But since growth and development of mosquito larvae were not measured, an interaction between mosquito larvae and tadpole species cannot be fully neglected. STAV et al. (2005) could show for *Culex pipiens* larvae that the presence of controphic species can increase time to metamorphosis and reduce size at metamorphosis. Similar effects could have occurred in the experiment although they have not been detected.

I could not confirm the assumption that the predatory *Hoplobatrachus occipitalis* tadpoles reduced mosquito numbers in ponds. But it has been observed that in median 4 of 5 mosquito larvae were consumed by *H. occipitalis* tadpoles in 1 L of pond water (NOPPER 2010). Likewise, MARIAN et al. (1983) could show that tadpoles of the related species *Hoplobatrachus tigerinus* efficiently reduced mosquito larvae numbers in a volume of 250 mL. In general, over 80% of larval mosquito mortality can be attributed to predation (MWANGANGI et al. 2008) and a total of approximately 250 predators of mosquito larvae (excluding fish) have been described (JENKINS 1964). Some of those seem to be more efficient predators than *H. occipitalis* tadpoles, but a comparison with other studies is difficult due to differences in experimental design. SERVICE (1970) reported on tadpoles of the genus *Ptychadena* feeding on *Aedes vittatus* larvae. Such predatory behaviour was not observed for *Ptychadena bibroni* tadpoles in the artificial ponds, but nevertheless could have occurred. Former studies have reported on the predatory potential of Notonectidae (KÖGEL 1984, BLAUSTEIN et al. 2004, 2005, ARAV & BLAUSTEIN 2006). Members of the Notonectidae have often been observed in the tanks. They could also have reduced mosquito larvae numbers. Their effect might even have exceeded the one of *H. occipitalis* as they were sometimes observed in higher numbers. However, the occurrence of potential predators of mosquito larvae was not assessed, neither quantitatively nor treatment specific, apart from *H. occipitalis*.

Oviposition avoidance by female mosquitoes in tanks, where *H. occipitalis* was present was not observed. ANGELON & PETRANKA (2002) assumed a threshold concentration of a possible cue, above which detection by the female mosquito could occur. Hence, densities of *H. occipitalis* (one individual per tank) might have been too low to get detected by female mosquitoes in the experiment. Nevertheless, in natural ponds these tadpoles do also not occur in high densities (own observation) and therefore stimulation of oviposition avoidance is very unlikely to take place. The finding that female *Anopheles gambiae* mosquitoes can detect competitors and avoid laying their eggs in the respective waters (MUNGA et al. 2006) could likewise not be verified, as the presence of none of the tadpole species was associated with the densities of mosquito larvae within ponds.

However, mosquito larvae assemblages included species that differed in their oviposition behaviour and larval biology. Mosquito larvae in large artificial ponds were predominantly *Anopheles* spp. (primarily *Anopheles gambiae* s.l.), whereas *Aedes* spp. (primarily *Aedes vittatus*) dominated mosquito larvae assemblages in small tanks. Abiotic factors that potentially could have influenced oviposition behaviour might have been more important in structuring mosquito larvae assemblages than possible interactions with the respective tadpole communities. The colour of the tanks (black for ST and light green for LT) could have influence oviposition choice of mosquito larvae as reported by MCCRAE (1984) and HUANG et al. (2005). Furthermore, depth could be another abiotic factor influencing their choice for oviposition. Water depth in small tanks was lower than in large tanks and thus might have been preferred for oviposition in *Aedes* larvae.

Although I could not prove any effects of tadpole species exclusion on mosquito larvae densities with the experimental trials, consequences of tadpole species losses on mosquito assemblages can not be neglected yet.

7 Final discussion

The present dissertation aimed to first analyse and evaluate the frog market in the West African countries Burkina Faso, Benin and Nigeria and second to investigate possible consequences for the ecosystem.

In all areas of investigation frogs were harvested and traded for human alimentation. The detected frog trade could be distinguished into three levels regarding its extent and its significance for the respective human population and for the respective ecosystem. The first level compasses the frog use in the province of Gourma, Burkina Faso. Here, the local population tended to catch and consume frogs rather occasionally and I concluded that the frog use was most probably sustainable at that time. There might have been an unsustainable use of frogs in the past since interviewees reported of declined frog numbers, which possibly led to a recession of frog use. Accordingly, I found lower species richness in this province compared to Ganzourghou.

The second level of frog trade was found in the province of Ganzourghou. Fishermen have been specialised in the collection and market-women in the preparation and selling of frogs on the local markets. The frog market included three levels of actors (collectors, market-women, and customers), who depended on the availability of the frogs and/or the income gained through the trade. I assume that the frog use in Ganzourghou was on the edge towards unsustainability. In case this market will increase the numbers of collected frogs will likely not be sustainable anymore and population numbers will decline.

The third and highest level of frog use concerned the trade in Nigeria. Apparently the frog trade has increased during the past five to ten years due to a growing demand for frogs in the southern cities of Nigeria. Most likely this growing demand for frogs was a result of the human population increase in this country, which was possibly attended by a decline of fish stocks. To meat the demand the frog trade already crossed the borders into neighbouring countries. The number of frog collectors and subsequently the amount of caught frogs already increased remarkable in Malanville, North Benin from 2008 to 2009. Regarding these high and still increasing numbers a sustainable use is most likely not given and declining population numbers have to be anticipated.

Overexploitation of amphibians is known from many different countries and regions worldwide but never has been reported for any countries or regions on the African continent. In cases where certain frog species have been exploited unsustainably I anticipated consequences for the lasting amphibian communities and for the ecosystem. Studies in India for instance concerning the consequences of the enormous frog trade in the 1970s and ‘80s revealed negative ecological and economical impacts due to dramatic declines of the collected frog species, which resulted in increasing insect pests and increasing usage of insecticides (ABDULALI 1985, OZA 1990). Adult amphibians are important as prey for various taxa (e.g. snakes, birds or mammals such as otters, DUELLMANN & TRUEB 1994, TOLEDO ET AL. 2007, VERBURG ET AL. 2007) and as predators (DUELLMANN & TRUEB 1994). VERBURG et al. (2007) encountered nitrogen isotope signatures of adult amphibians that pointed to an insectivorous diet. A study by HIRSCHFELD & RÖDEL (submitted) revealed a broad range of different taxa consumed by *Hoplobatrachus occipitalis* adults such as Coleoptera, Lepidoptera, spiders, Formicidae, or fishes. Furthermore, VERBURG et al. (2007) have pointed out that amphibian losses probably result in changes in processes and functioning such as nitrogen-cycling and energy exports to riparian food webs. In case of an altered amphibian diversity ecosystem processes will be affected not only in terrestrial ecosystems but also in freshwater ecosystems since tadpoles play important roles in nutrient and energy cycles in freshwater habitats (e.g. SEALE 1980, KUPFERBERG 1997, FLECKER et al. 1999, RANVESTAL et al. 2004).

Harvesting of adult amphibians could have affected tadpole composition by taking specific species out of the environment in high numbers (MILNER-GULLAND 2008). This especially concerned *Hoplobatrachus occipitalis,* which was by far the most collected and traded species in all areas of investigation. Lower occurrence rate of these tadpoles in the disturbed area in Ganzourghou could be a direct effect of harvesting in this area.

My study revealed lower species richness and a different species composition of tadpoles in anthropogenic disturbed areas in the West African savanna regions, where frogs were collected. In some cases not only some species but a whole genus showed lower occurrences in disturbed areas. Tadpole genera that were predominantly underrepresented in disturbed areas were *Afrixalus*, *Hyperolius*, *Leptopelis*, *Hoplobatrachus*, and *Ptychadena.* However, apart from *H. occipitalis* and *Ptychadena* spp., those amphibians were not used for consumption and thus were not subject of harvest activities. Thus, causes other than overexploitation had to be responsible too for different assemblage structures between disturbance regimes.

Despite a possible impact of harvesting on the occurrence of particular species, I identified environmental parameters to explain main differences in assemblage structures between disturbance regimes. Predominantly, the habitat surrounding the breeding ponds including different vegetation structures, such as amount of trees, shrubs and high or low grass plants, correlated with the composition of tadpole assemblages. Hence, the adult habitat seemed to be a decisive factor for structuring tadpole communities. Changes in habitat factors were probably due to anthropogenic impact including agriculture and livestock herding. Alterations of habitat factors mainly affected the adult amphibian community and consequently altered tadpole assemblages. Especially species depending on terrestrial vegetation such as

Afrixalus, *Hyperolius*, and *Leptopelis* were likely affected by these alterations and indeed showed major differences in their frequency of occurrences between disturbance regimes.

Since entire genera were affected by disturbance, effects concerning functional diversity were likely too. Former studies on amphibian assemblages in relation to anthropogenic disturbances have reported of group-specific differences in responds to habitat alterations (ERNST et al. 2006, ERNST & RÖDEL 2008). Specific functional groups are hence more affected by anthropogenic disturbance than others resulting in an altered functional diversity in disturbed regions. Furthermore, the loss of diversity to the point that entire functional effect groups disappear, could have the greatest impact on ecosystem processes and will further affect ecosystem functions (HOOPER et al. 2002, DOWNING 2005).

Disturbance events (such as overexploitation, habitat fragmentation and agricultural practises) not only lead to a decline in biodiversity but may also change food web structures including the relative influence of top-down and bottom-up forces. The effects of biodiversity loss in freshwater ponds could further be to dislocate food chains or change trophodynamics in subtle and unexpected ways (RAFFAELLI et al. 2002). I anticipate differences in food web structures and trophic cascading particularly between ponds of disturbed areas. Similarly, PETCHEY et al. (1999) showed with an experimental approach that extinctions were more frequent in disturbed treatments (due to warming) and were trophic level dependent, with changes in food web structure having likely effects on ecosystem processes (primary production).

I conducted the species exclusion experiment to investigate the effect of the presence and absence, respectively, of particular tadpole species on the remaining tadpole community, including their survival, growth, development and trophic ecology. With the experimental approach I revealed a changed functional diversity in case of species exclusion. I was able to show that tadpoles of different anuran species have different trophic positions and functions in the pond ecosystem and hence play different ecological roles. Various complex interactions between the tested species were detected. Isotope analysis revealed variation in intra-specific isotope signatures in some species according to the respective tadpole assemblages, thus showing that food web functioning can change depending on the presence and absence of particular tadpole species.

Within this experimental approach, tadpoles of *H. occipitalis* have been identified as top-predators in freshwater ponds' food webs. I found altered survival rates in co-occurring species of different trophic positions (filter-feeders, herbivorous) in absence of *H. occipitalis* tadpoles. Survival rates of tadpoles furthermore differed between the species of the other trophic levels, with *Phrynomantis microps* (filter-feeders) showing lowest and *Kassina fusca* (herbivorous) highest survival rates in presence of the predator. The predator seemed to have an important role in controlling the numbers of herbivorous and filter-feeding tadpole.

By reducing their numbers, phytoplankton and periphyton growth rates increase and provide enough food for surviving tadpoles.

In the absence of the predator, density effects may account for altered species composition. Increasing densities can lead to an increase of intra- and interspecific competition of prey species, due to a decrease in food availability, followed by lower development and growth rates and therewith a changing time to metamorphosis in particular species (e.g. WILBUR 1987, SKELLY 1997, FLECKER et al. 1999, LOMAN 2001, 2004, RUDOLF & RÖDEL 2005). Hence, the eradication of *H. occipitalis* might lead to density effects with possible cascading extinctions, which could exceed pure predatory effects (THÉBAULT et al. 2007). In case of harvesting *H. occipitalis,* a decline of this top predator in temporary ponds may succeed and accordingly influence the remaining tadpole assemblages (higher survival rates but probably also higher rates of competition). Overexploitation is thus one possible cause for altered amphibian assemblages and subsequent ecosystematic consequences in disturbed areas.

Tadpoles of *H. occipitalis* contribute to ecosystem functioning in ways that are unique, thus their loss causes detectable changes in functioning. However, there were areas, where *H. occipitalis* seemed to not occur naturally. I did not detect its tadpoles in ponds of the undisturbed area in Gourma (Reserve de Pama) probably due to a lack of suitable water bodies to overcome the dry season. Hence there seemed to be ecosystems existing without the top-down control of this particular predator. Other taxa such as invertebrates (e.g. dragonfly larvae) could have possibly taken over this trophic position in those freshwater ponds.

Generally, I could show that the absence of a particular species, and a trophic position respectively, could lead to alterations in feeding behaviour of remaining tadpole species. *K. fusca* tadpoles seemed to switch to more omnivorous diet in treatments without the predator. Furthermore, nitrogen isotope signature of *Ptychadena bibroni* tadpoles decreased in treatments without *K. fusca*. Hence, herbivorous tadpoles of *K. fusca* might have competitive effects on *P. bibroni*, indicating that some of the same resources were probably used by both species but under different circumstances. Compensatory interactions are known to occur within a trophic level in aquatic systems (see RAFFAELLI et al. 2002). In an experiment by LEIBOLD & WILBUR (1992) for example, a planktonic herbivore (*Daphnia*) enhanced periphytic growth, whilst a surface grazer (*Rana*) enhanced phytoplankton growth.

Consequently, shifts in trophic positions are possible in altered amphibian communities (VERBURG et al. 2007). This could have been taken place also in natural ponds.

Tadpole assemblages of the natural ponds in Burkina Faso varied in their composition and sometimes particular trophic levels were not represented as the respective tadpole species have not been detected. Tadpoles of the species *Ptychadena bibroni*, *P. tellini*, *P. tournieri*, and *P. trinodis* showed lower frequencies of occurrence in disturbed areas in Ganzourghou.

These species were also collected for consumption, which could have potentially caused their lower presence in that area. In ponds where *P. bibroni* was missing, its trophic position was probably occupied by other species of this genus since species of this genus usually occurred in different ponds (own observation). However, in ponds where the whole genus was absent, the respective trophic level might have been absent too, given that no tadpoles of other genera might have taken over that particular trophic position. Generally, in areas where a particular trophic level was not represented because the species belonging to this trophic level did not occur or were underrepresented, as it was the case for *H. occipitalis* and various *Ptychadena* species in disturbed areas, alterations in the feeding ecology possibly appeared. Herbivorous tadpoles of the genus *Kassina*, however, showed no difference in their occurrences between disturbance regimes. Hence, anthropogenic activity and altered tadpole assemblages seemed to have no effect on the presence and absence of this genus but shifts in their diet due to the respective assemblage composition were likely as were shown with the species exclusion experiment.

In artificial ponds the presence of *P. microps* had an indirect beneficial effect on the survival of the other species, mainly of *P. bibroni*. In ponds where *P. microps* was absent significantly less tadpoles of *P. bibroni* survived until the end of the experiment. The loss of *P. microps* also could lead to a higher predation pressure on tadpoles of other anuran species in natural ponds. I encountered natural ponds where *P. microps* tadpoles were absent and tadpoles of *H. occipitalis* were present indicating a possible susceptibility to predation also in natural ponds. In those ponds tadpoles of the genera *Kassina* and *Ptychadena* were present. Furthermore, tadpoles of *P. microps* occurred more often in ponds of the disturbed areas, where tadpoles of *H. occipitalis* were found less often. This was also the case for the filter-feeding tadpoles of *Xenopus muelleri.* Hence filter-feeders might have had an advantage in ponds of disturbed areas based on lower occurrence rates of potential predators. However, larvae of *X. muelleri* are fast swimmers in comparison to *P. microps* and are thus not a similar easy prey. Besides lower occurrence rates of potential predators, a higher nutrient input by livestock could be a reason for the presence of *X. muelleri*, and filter-feeders in general, in disturbed areas and their absence in undisturbed areas. The nutrient input by wild animals in undisturbed areas might be too irregularly in comparison to the input by domestic animals in disturbed areas, which often visit particular ponds on a daily basis.

An actual filter-feeding effect was shown for *P. microps* tadpoles in artificial ponds, where water transparency was significantly higher in presence of the filter-feeder than without it.

Besides filter-feeding tadpoles, larvae of the mosquitoes *Anopheles* and *Culex* are also filter-feeders. *Anopheles* larvae occurred less in disturbed areas, hence might have been disadvantaged in the competition about resources with co-occurring taxa of the same trophic level, such as *P. microps* and *X. muelleri*. Therefore, the harvesting of *H. occipitalis* might have actually led to a reduction of *Anopheles* larvae in the disturbed area. *Anopheles* mosquitoes transmit the parasite *Plasmodium*, which is the agent of malaria. Hence, the human population may even have an indirect advantage from the frog trade since the Malaria rate in their villages could be subsequently lowered. However, there was no effect of altered tadpole assemblages on mosquito larvae assemblages detected in artificial ponds. Predominantly mosquito larvae of the genera *Anopheles* and *Aedes* were found in artificial ponds. As those two genera were found more often in undisturbed areas it could have been possible that the artificial ponds rather resembled natural ponds habitat rather than ponds in villages. Concerning mosquito larvae assemblages in natural ponds I encountered local differences, with *Anopheles* and *Aedes* larvae found more often in undisturbed areas and *Culex* larvae more often in disturbed areas. There was a trend visible that certain tadpole community compositions simultaneously favoured specific mosquito larvae assemblages (compare with Mantel test, Chapter 5). KIFFNEY & RICHARDSON (2001) assumed that tadpoles interact with controphic species via resource competition and interference. It is therefore possible that mosquito assemblages were determined to a certain extent by tadpole assemblages although I could not prove this interaction in the experiment. Tadpole assemblages, on the other hand, were probably rather structured by environmental parameters. This is in accordance with former studies, which stated that presence and absence of tadpole species are usually based on abiotic factors and species abundances are rather limited by biotic factors (predation, competition etc.) (e.g. SCHNEIDER & FROST 1996). In this respect I would recommend obtaining abundance data of tadpoles and of mosquito larvae in order to detect possible interspecific effects in more detail.

Alterations of habitat factors due to anthropogenic activity were proven to be responsible for differences in tadpole species composition and occurrences of particular species particularly for species, which adults depend on terrestrial vegetation. Overexploitation as a reason for species absences as well as for altered community compositions could not be fully verified yet it can also not be refused. Furthermore, there is evidence that the harvesting and consumption of frogs is going to increase. Hence, the impact will likewise increase and amphibian communities will fall even more prey to alterations. The resulting consequences of altered tadpole assemblages will increase in intensity and other consequences, not observed in this study, are also possible. Fact is that tadpole species showed different occurrence rates depending on region and disturbance regime. NAEEM et al. (1994) stated that loss of biodiversity, in addition to loss of genetic resources, loss of productivity, loss of ecosystem buffering against ecological perturbation, and loss of commercially valuable resources, may also alter or impair the services that ecosystems provide under pristine circumstances. If we consider that species belonging to the same trophic guild would represent one functional group, then effects of disturbances can be translated into effects in terms of altered contributions to ecosystem processes (DE RUITER et al. 2002). These effects could be particularly true, where *H. occipitalis* tadpoles as top predators are absent due to anthropogenic impact.

In West Africa, amphibians are important for the local human population. The ethnozoological data I could obtain from the interviews showed the importance of various frog species in human culture, livelihood and as a protein source in particular. Moreover, in TYLER et al. (2007) we find a summary of benefits and importance of amphibians for humans encompassing food, sources of medicinal preparations, and model organisms in biological research and pharmacology. It is thus important to preserve healthy amphibian communities and the ecosystem they live in, in order to preserve ecosystem services. Therefore, conservation actions should be conducted in order to avoid an overexploitation of certain frog species and the resulting consequences in West Africa. Herein I recommend the following conservation and research activities:

Recommendations:

- The basic biology and natural history of the harvested species, predominantly of *Hoplobatrachus occipitalis*, (e.g. life expectancy, mortality and fecundity) needs to be better understood.
- The community organisation in general (top-down and bottom-up effects between trophic levels) needs to be better understood to be able to better evaluate effects on ecosystem processes and thus on ecosystem functions. Isotopic analyses of the whole community would be one step in this direction.
- The motivation of the people who are exploiting the species has to be carefully considered and alternative labour options should be reflected.
- Further investigation of the amphibian trade especially in Nigeria, but as well in other neighbouring countries such as Niger and Chad should be carried out to completely overview the dimension of the frog trade in West Africa.
- When overexploitation is likely, the respective authorities need to be informed to start monitoring the collection and to imply harvesting rules (harvest only at particular places, certain seasons etc.).
- Public awareness concerning the role of amphibians and their ecosystem services should be raised locally.
- Inquiries to cultivate the native *Hoplobatrachus occipitalis* involving local stakeholders should be undertaken. To hold up their livelihood former frog collectors could be acquaint with this task.

- Further surveys of the amphibian fauna of the respective areas need to be carried out. To be able to spot declining species and changes in assemblage compositions easier, I highly recommend obtaining abundance data instead of presence / absence data.
- Surveys should be also undertaken in areas with high harvest rates, such as in the surrounding area of the Niger River in Benin, Nigeria and Niger. As the amount of harvested *H. occipitalis* in North Benin exceed the harvest numbers in Burkina Faso, possible consequences concerning remaining amphibian communities and effects of ecosystem functions are probably more noticeable and easier to detect in this region.

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Appendix 1

Fiche d'enquête pour des villageois en Burkina Faso

a. ID-Nr.:

b. Date:…………………………………………………………
c. Village:………………………………………………………
d. Interviewer:…………………………………………………

Informant:
e. Age/Date de naissance:………………………………………
f. Sexe:…………………………………………………………
g. Ethnie:………………………………………………………..
h. Religion:……………………………………………………...
i. Statut social:…………………………………………………..
j. Membres de ménage**:** Total………; Adultes…….. (male……..femelle…….);

Enfants……..

1. Effet d'exploitation des grenouilles

1.1. Quelle source d'eau est-ce que vous utilisez?
1. Puits **2.** Barrage **3.** Rivière /fleuve **4.** Étang

1.2 Si pas d, est-ce qu'il y a des situations ou on utilise aussi l'eau des ponds temporaire? Et pour quelle raison?

1.3. Est-ce que vous avez remarqué un changement de qualité de l'eau?

1. Plus turbide/sale/trouble? **2.** Plus d'algues (coloration verte)? **3.** Changement de goût?
4. Autre:

1.4. Est-ce que le nombre de moustiques a augmenté par rapport au passé ?
1. Oui, distinct **2.** Oui, un peu **3.** Non, comme toujours **4.** Non, ils ont même diminué

1.5. Est-ce que vous avez remarqué une hausse de maladies fiévreuses?

1.6. Si oui, de quelles maladies?

2. Dimension de la consommation des grenouilles

2.1. Les grenouilles sont-elles consommées dans ce village (cette ville)?

2.2. Est-ce que votre ménage consomme des grenouilles?

2.3. Si non, Quelles sont vos raisons pour ne pas consommer des grenouilles?

2.4. Si oui, pouvez-vous estimez combien de kg de grenouille votre ménage consume par semaine?

2.5. Ca fait combien de pourcents de la consommation totale des produits animaux?

2.6. Les espèces consommées (Photos)
1. *H. occipitalis* uniquement? **2.** Autres espèces?
Lesquelles……………………………………………………………………….

2.7. Les espèces de crapaud aussi?

2.8. Quelle est la taille préférée pour la consommation?
1. Grande (adulte) **2.** Petite (jeun adulte) **3.** Toute taille confondue

2.9. Y a-t-il un sexe préféré?

2.10. Les grenouilles sont-elles vendues également sur le marché?

2.11 Avec quelle quantité de mesure?
1. Kilo **2**. Sac **3**. Plat
Volume du sac ou du plat:…………………………Et le prix…………………………..

2.12 Est-ce qu'ils sont aussi capturés par vous-même?
Si oui, continue avec chapitre 2

2.13 Si non, D'où obtenez-vous normalement des grenouilles?
1. Collecteur **2.** Cadeau **3.** Sur la voie **4.** Marches **5.** Magasins **6.** Autre

3. Capture des grenouilles

3.1 **Lieu de capture des grenouilles?** (si il y a plusieurs lieu, quelle quantité est capturer ou (proportionnel))
1. Mare (permanent) **2.** Mare (temporaire) **3.** Rivière **4.** Barrage
5. Autres endroits possibles:……………………………………………

3.2 A quelle distance du village?
1. Loin (> 1km) **2.** À côté (< 1km)

3.3 Pendant quelle période de l'année sont capturées les grenouilles?
1. Saison sèche **2.** Saison pluvieuse **3.** Toute l'année

3.4 Est-ce qu'il y a un période où la capture est interdite et pourquoi?
Si oui, raison:……………………………………………………………

3.5 A quelle période de la journée?
1. Matin **2.** Soir **3.** Toute la journée **4.** Nuit

3.6 Méthode de capture
1. A la main **2.** Avec un filet **3.** Avec un hameçon
4. Avec une nasse
5. Autre:…………………………

3.7 Situation des individus capturant les grenouilles
(Sexe, Age, Ethnie, Statut social)

3.8 Comment êtes-vous arrivé à cette activité?
1. Héritage **2.** Conseil d'un ami **3.** Initiative personnelle
4. Autres (préciser)…………………… …………………

3.9 Quelle place occupe ce commerce dans vos activités?
1. Premier **2.** Deuxième **3.** Autre (préciser)

4. Signification socio-économique

4.1 Le plus important avantage des grenouilles (notation 1-3, 1 = plus important)
1. Consommation **2.** Vente **3.** Remèdes

Vente
4.2 Où retrouve- t-on les grenouilles vendues? (où sont-elles vendues?)
1. Au marché **2.** Au restaurant **3.** À la maison **4.** À l'hôtel
5. Autres lieux de vente:…………………………………………………

4.3 Elles sont vendues à qui? (notation) **Et combien?**
1. Villageois **2.** Passagers **3.** Résidents dans les hôtels
4. Autre…………..

4.4. Le prix de vente:…………………………

4.5 Les prix sont-ils stables ou fluctuants?
1. Stables **2.** A la baisse **3.** A la hausse

4.6 Situation des individus chargés de la vente des grenouilles:
(Sexe, Age, Ethnie, Statut social)

Consommation

4.7 Partie consommée:
1. Cuisse **2.** Cuisses et tronc **3.** Tout le corps

4.8 Si une partie est consommée, que fait-on du reste?
1. Jeté **2.** Donné aux animaux domestiques **3.** Autres usages:…………………

4.9 Comment les consommez-vous (recette)?

4.10 Combien des grenouilles on a besoin pour un repas?

4.11 Combien des fois par semaine / par mois vous consommez des grenouilles?

4.12 Est-ce qu'on a toujours consommé les grenouilles?

4.13 Si non, est-ce que la consommation des grenouilles était apparue avec l'arrivée des étrangers?

4.14 Est-ce que vous préférez des grenouilles avant l'autre viande/poisson?

Avantages culturels

4.14 Pour quel usage culturel (mise a part la consommation nutritionnel) la grenouille ou le crapaud sont utilises?
1. Fétiche **2.** Médicament **3.** Nourriture lors des cérémonies
4. non usage culturel **5.** Autre……………………………………………………………

4.15 Quelle espèce?
1. Grenouille **2.** Crapaud
Espèce exactement (Photo):………………………………………………

4.16 Manier du remède (quelle partie de grenouille /crapaud est utiliser et qu'est-ce qu'on fait avec ca)?

5. Accessibilité des grenouilles

5.1 Y a-t-il des lieux sacrés où la capture des grenouilles est interdite?

5.2 Certaines espèces sont-elles plus difficiles à trouver aujourd'hui qu'autrefois?
Si non, continue avec 5.7

5.3 Si oui, pourquoi?

5.4 Quelle espèce?

5.5 Depuis quand?

5.6. Quelle différence y a-t-il entre le nombre actuel de grenouille capturées et avant?

5.7. Imaginez vous qu'il soit possible d'élever des grenouilles (pour la consommation)?

Fiche d'enquête sur des marchés

ID-Nr.:

Date:……………………………………………………………
Village:…………………………………………………………
Interviewer:……………………………………………………….

Informant:
Age/Date de naissance:………………………………………...
Sexe:……………………………………………………………
Ethnie:………………………………………………………….
Religion:………………………………………………………
Statut social:…………………………………………………

1. Vendeur

1.1. Pendant quelles saisons vous êtes ici pour vendre des grenouilles?
1. Saison sèche **2**. Saison pluie **3**. Toute l'année

1.2. Pendant cette temps, combien de fois vous êtes ici pour vende des grenouilles?
(Par semaine, mois, année)

1.3. Des grenouilles sont vendues à qui? (ordre)
1. Villageois **2.** Passagers **3.** Résidents dans les hôtels **4.** Autre………

1.4. Le prix de vente actuellement:…………………………

1.5. Est-ce que le prix dépendant au client?

1.6. Les prix sont-ils stables ou fluctuants?
1. Stables **2.** A la baisse **3.** A la hausse

1.7. Combien des grenouilles vous vendrez au général? (no. des plates / sacs / kilos)

1.8 Qui a capture des grenouilles? Même famille?
(Age, Sexe, Ethnie, Religion, Statut Social)

1.9 Si pas de même famille, de qui et pour combien vous avez acheté les grenouilles?

1.10 Quelles espèce est-ce que vous vendrez? (Toujours les même espèces ou c'est variable?)

1.11 Est-ce vous avez traits des grenouilles?

1.12 Si oui, comment?
1. Séchés **2.** Fumés **3.** Salé **4**. Autres……………

Fiche d'enquête pour des pêcheurs en Burkina Faso et Bénin

a. ID-Nr.:

b. Date:……………………………………………………………
c. Place / Village:…………………………………………………
d. Interviewer:………………………………………………………

Informant:
e. Age/Date de naissance:………………………………………
f. Sexe:……………………………………………………………
g. Ethnie:…………………………………………………………
h. Religion:………………………………………………………
i. Statut social:…………………………………………………
j. Membres de ménage**:** Total………; Adultes…….. (male……..femelle…….);

Enfants……..

1. Dimension de la pêche des grenouilles

1.1 Est-ce que vous connaissez ces espèces des grenouilles? Photos

1.2. Quelles espèces sont consommées? (Photos)

1.3. Les espèces de crapaud aussi?

1.4. Et quelles espèces est-ce que vous capturez pour la vend?

1.5. Quelle est la taille préférée pour la capture/vend?

1. Grande (adulte) **2.** Petite (jeun adulte) **3.** Toute taille confondue

1.6. Y a-t-il un sexe préféré?

1.7. Pouvez-vous estimez combien des grenouilles vous capturez par semaine (nombres / kilo / sacs)?

2. Capture des grenouilles

2.1 Paye, région, place de capture des grenouilles? (si il y a plusieurs places, quelle quantité est capturer ou (proportionnel)

2.2 Lieu de capture des grenouilles? (si il y a plusieurs lieu, quelle quantité est capturer ou (proportionnel))
1. Mare (permanent) **2.** Mare (temporaire) **3.** Rivière **4.** Barrage
5. Autres endroits possibles :……………………………………………

2.3 Pendant quelle période de l'année sont capturées les grenouilles?
1. Saison sèche **2.** Saison pluvieuse **3.** Toute l'année

2.4 Est-ce qu'il y a un période où la capture est interdite et pourquoi?
Si oui, raison:…………………………………………………………

2.5 A quelle période de la journée?
1. Matin **2.** Midi **3.** Soir **4.** Toute la journée **5.** Nuit

2.6 Méthode de capture
1. A la main **2.** Avec un filet **3.** Avec un hameçon
4. Avec une nasse
5.Autre:………………………………………………………………………………..

2.7 Combien des grenouilles est-ce que vous pouvez capturez avec cette méthode par fois?

2.8 Situation des individus capturant les grenouilles
(Sexe, Age, Ethnie, Statut social, Autre)

2.9 Comment êtes-vous arrivé à cette activité ?
1. Héritage **2.** Conseil d'un ami **3.** Initiative personnelle
4. Autres (préciser)……………………. …………………

2.10 Quelle place occupe ce commerce dans vos activités?

1. Premier **2.** Deuxième **3.** Autre (préciser)

3. Signification socio-économique

3.1 Le plus important avantage des grenouilles (notation 1-3, 1 = plus important)
1. Consommation **2.** Vente **3.** Remèdes

Commerce
3.2 Ou ventez-vous des grenouilles?

3.3 Si c'est an autre paye, est-ce vous dois payer des douanes?

3.4. A qui ventez-vous des grenouilles?

3.5 Comment ventez-vous des grenouilles? Est-ce qu'ils sont encore vivants ou traitez-vous des grenouilles avant de vendre?

3.6 Quelle quantité des grenouilles ventez-vous également? (nombre, kilogrammes, sacs, etc.)

3.7 Tous les combiens ventez-vous des grenouilles? (per semaine, mois, année)

3.8 Est-ce que vous capturez des grenouilles sur commande?

3.9 Combien des grenouilles (kilo, sac, nombre etc.) comportent une commande / livraison au général?

3.10 Et combien des fois par mois vous livrez?

3.11 Pour combien ventez vous les grenouilles?

3.12 Les prix sont-ils stables ou fluctuants
1. Stables **2.** A la baisse **3.** A la hausse

3.13 Où retrouve- t-on les grenouilles vendues ? (où sont-elles vendues?
1. au marché **2.** au restaurant **3.** a la maison **4.** à l'hôtel
5. cabaret /bar
6. Autres lieux de vente:……………………………………………

3.14 Situation des individus chargés de la vente des grenouilles
(Sexe, Age, Ethnie, Statut social, Autre)

4. Accessibilité des grenouilles

4.1 Y a-t-il des lieux sacrés où la capture des grenouilles est interdite? (Ou ?)

4.2 Certaines espèces sont-elles plus difficiles à trouver aujourd'hui qu'autrefois?
Si non, continue avec 5.7

4.3 Si oui, pourquoi?

4.4 Quelle espèce?

4.5 Depuis quand?

4.6. Quelle différence y a-t-il entre le nombre actuel de grenouille capturées et avant?

4.7. Imaginez vous qu'il soit possible d'élever des grenouilles (pour la consommation)?

Questionnaire for the frog-collectors

- **Presentation**
- **Outline the aims of the questionnaire**
- **Explain that it is anonym (the data will be treated confidential)**

a. ID-Nr.: F-xy

b. Date:…………………………………………………………….
c. Place:……………………………………………………………
d. Interviewer:…………………………………………………..

Informant:
e. Age /Date of Birth:…………………………………………...
f. Sex:……………………………………………………………
g. Ethnic:……………………………………………………….
h. Religion:…………………………………………………….
i. Social Status / Occupation:……………………………………………………
j. Members of household**:** Total………; Adults…….. (male……..female…….);

Children……..

1. Dimension of the frog collection

1.1 Are you familiar with these frog species? (photos)

1.2. Which are the species used for consumption? (Record the number of the photo)

1.3. Toad species, too?

1.4. And which species do you capture particularly for sale? (Record the number of the photo)

1.5. Which body sizes are preferred to catch?
1. Large (adult) **2.** Small (young adult) **3.** All sizes are caught

1.6. Is one sex preferred over the other?

1.7. Could you please estimate the quantity of frogs you collect every day / week / month? (Number / kg / sacks)

2. Methods of frog collection

2.1 Where are the frogs collected (country, region, town)? (if more than one place, which quantity is caught at which place (proportionally)?)

2.2 From which environment / habitat are the frogs collected (if more than one place, which quantity is caught at which place (proportionally)?)
1. Pond (permanent) **2.** Pond (temporary) **3.** River **4.** Reservoir
5. Other places:…………………………………………

2.3 During which season of the year are the frogs caught?
1. Dry season **2.** Rain season **3.** All year round

2.4 Is there a time period when it is forbidden to catch frogs?
If yes, reason:…………………………………………

2.5 At which time of the day do the frogs get caught?
1. Early morning **2.** Midday **3.** Evening **4.** All day round **5.** Night

2.6 Method of collection (if more than one list by importance)
1. Hands **2.** Fishing net **3.** Hooks
4. Basket trap **5.** Other:……………………………………

2.7 How many frogs are you able to collect at once using this method?

2.8 Who is able / is allowed to collect frogs?
(Sex, Age, Ethnic group, Social Status, Other)

2.9 How did you get to this activity?
1. Heritage **2.** Someone's advise **3.** Own initiative
4. Other (explain)…………………….

2.10 Which rank does this activity occupy between your other activities?

1. First **2.** Second **3.** Other (explain)

3. Socio-economical signification

3.1 The most important advantage of frogs (notation 1-3, 1 = most important)
1. Consumption **2.** Sale **3.** Medicine

Commerce

3.2 Where do you sell the frogs? (Give name of exact localities)

3.3 In the case that the location is in another country, do you have to pay tax fees at the border?

3.4 Whom do you sell the frogs?

3.5 How do you sell the frogs? Are they still alive or do you treat them in any form?

3.5 Which quantity of frogs do you usually sell? (number, kilograms, sacks, etc.)

3.6 How often do you offer/sell?

3.7 Do you capture and sell frogs also by order? If not, continue with 3.10

3.8. If yes, how many frogs (number / kg / sacks) are generally included in one order/delivery?

3.9 How often do you deliver during one month?

3.10 For how much do you sell the frogs (prices)?

3.11 Are the prices stable or did they increase or decrease over time?
1. Stable **2.** Decreasing **3.** Increasing

3.12 Where can you regain the frogs afterwards?
1. market **2.** restaurant **3.** someone's place **4.** hotel
5. bar / pub **6.** Other places (specify)

3.13 Who is able / is allowed to sell frogs?
(Sex, Age, Ethnic, Social Status, Other)

4. Accessibility of frogs

4.1 Do you know of a place where it is forbidden to capture frogs?
If yes, where?

4.2 Do you know of frog species which numbers are declining or might be even locally extinct?
If not, continue avec 5.7

4.3 If yes, which species?

4.4 Are these species declining everywhere or is it locally restricted? If locally restricted, specify the area / region.

4.5 Do you have an idea, why they are declining?

4.6 Can you estimate to which extent the numbers of these species are declined?

4.7 Since when did you noticed the species' decline?

4.8. Could you imagine breeding frogs (for consumption)?

Questionnaire for the frog-traders

- **Presentation**
- **Outline the aims of the questionnaire**
- **Explain that it is anonym (the data will be treated confidential**

a. ID-Nr.: T-xy

b. Date:…………………………………………………………………
c. Place:………………………………………………………………
d. Interviewer:……………………………………………………….

Informant:
e. Age /Date of Birth:………………………………………...
f. Sex:……………………………………………………………….
g. Ethnic:………………………………………………………….
h. Religion:……………………………………………………….
i. Social Status / Occupation:……………………………………………………
j. Members of household**:** Total………; Adults…….. (male……..female…….);

Children……..

1. The Species

1.1 Which are the frog species you are dealing with? (Photos)

1.2 Are you also dealing with toad species?

1.4. If more than one species: Is one species preferred over the others?

1.5 If yes, which species?

1.5 Do you trade frogs during a specific period of the year?
1. During dry season **2.** During rain season **3.** All year round
4. Other (specify)

1.6. Do you know where the frogs got collected? (Country, region, place)

1.7Are the frogs still alive or are they treated in any form when you trade them? (Specify)

2. The trade

2.1 For which purpose do you trade the frogs? (if more than one, list by importance)
1. Consumption **2.** Medicine **3.** Souvenirs **4.** Other (specify)

Purchase

2.2 Where do you buy the frogs? (Country, region, place)

2.3 If in another country, why? If not continue with 2.5

2.4 Do you have to pay tax fees when crossing the border?

2.5 From whom do you buy the frogs?
1. Collectors **2.** Other trader **3.** Market seller **4.** Other (specify)

2.6 Which quantity of frogs do you usually deal with? (number, kilograms, sacks)

2.7 How often do you usually purchase frogs?

2.7 What is the purchase price?

2.8 Is this price variable or stable?
1. variable **2.** stable

2.9 If variable, on what does it depend on?

2.10 Did the prices increased or decreased over the years?
1. Increased **2.** Decreased **3.** Neither (more or less stable over the years)

Sale

2.11 Where do you resell the frogs? (Country, region, place)

2.11 Who are the frogs get sold? Who are your customers? (If more than one, list by importance)
1. Market salesman, -woman **2.** Shop salesman, -woman **3.** Restaurant **4.** Hotel
5. Bar, pub **6.** Other trader **7.** Other (specify)

2.12 Are they regular customers or do the customers vary?

2.13 Are you usually able to resell the quantity of frogs you gained all at once?

2.14 If not, in which quantities do you resell the frogs?

2.15 What is the sales price?

2.16 How does the sales price depend on the purchase price?

2.17 Do you receive orders from your customers?

2.18 If yes, how often do you receive an order per week/month/year?

2.19 How many frogs (number, kilograms, sacks etc.) does an order usually contain?

Questionnaire for the market-salesperson

- **Presentation**
- **Outline the aims of the questionnaire**
- **Explain that it is anonym (the data will be treated confidential)**

a. ID-Nr.: M-xy

b. Date:……………………………………………………………
c. Place:…………………………………………………………
d. Interviewer:………………………………………………………

Informant:
e. Age /Date of Birth:…………………………………………...
f. Sex:……………………………………………………………
g. Ethnic:…………………………………………………………….
h. Religion:………………………………………………………….
i. Social Status / Occupation:………………………………………………………
j. Members of household**:** Total………; Adults…….. (male……..female…….);

Children……..

1. Market Sale

1.1. During which season you are here to sell frogs?
1. Dry season **2**. Rain season **3**. All year round

1.2. During this time, how often you are here to sell the frogs? (per week, month, year)

1.3. Do you sell the frogs also on other markets than this one?

1.3. Who do you sell the frogs?
1. Habitants **2.** Passengers **3.** People from restaurants/hotels
4. Other………

1.4. What is the actual sales price?:…………………………

1.5. Does the price depend on the customer?

1.6. Are the prices variable or stable?
1. Stable **2.** Increasing **3.** Decreasing

1.7. How many frogs do you usually sell per day? (Number, kilograms, sacks)
If the quantity is not known, ask for how much they sell per day.

1.8 From whom did you get the frogs?
1. Collector **2**. Trader **3**. Family member **4**. Other

1.9 For how much did you purchased the frogs?

1.10 Which species do you usually sell? (Photos)

1.11 If more than one species, is there one species preferred for sale?

1.11 Do you treat the frogs before you sell them?

1.12 If yes, how?
1. Dried **2.** Smoked **3.** Salted **4**. Fried **5**. Other…………….

Questionnaire for the customers/consumers

- **Presentation**
- **Outline the aims of the questionnaire**
- **Explain that it is anonym (the data will be treated confidential**

a. ID-Nr.: Cu-xy

b. Date:………………………………………………………………
c. Place:……………………………………………………………
d. Interviewer:………………………………………………………

Informant:
e. Age /Date of Birth:…………………………………………...
f. Sex:………………………………………………………………
g. Ethnic:…………………………………………………………….
h. Religion:………………………………………………………….
i. Social Status / Occupation:……………………………………………………
j. Members of household**:** Total………; Adults…….. (male……..female…….);

Children……..

1. Customer/Consumer

1.1. For what reason do you acquire frogs?
1. Own consumption **2.** To offer in a restaurant **3.** To offer in a hotel
4. To prepare for friends/family **5.** Other

1.2 How do you receive the frogs?
1. By buying **2.** By ordering in a restaurant **3.** By collecting oneself (continue with chapter 3)

Customer

1.2. How many frogs do you acquire at once?

1.3. How often do you acquire frogs? (how many times per week, month, year)

1.4. Where do you go to buy the frogs? (If more than one place, list by importance)

1.5. From whom do you buy the frogs there?

1.6. Do you usually command a specific quantity? If no, continue with 1.7

1.6.1. If yes, for how much do you usually command?

1.6.2. And how often do you command?

1.7. What is the price you normally pay?

1.8. Has the price always been like that?

1.9. If no, how did it change?
1. Increased **2.** Decreased **3.** Varies depending on the season

1.10. Which are the frog species you usually buy? (Photos)

1.11. If more than one species, is there one species preferred?

2. Consumption

2.1 At home

2.1.1 How often do you consume frogs?

2.1.2 How many frogs do you usually consume by yourself or in your family?

2.1.3. Which are the body parts you consume?
1. Legs **2.** Trunk without head **3.** Whole frog

2.1.4 If not the whole body what do you do with the rest?

2.1.5 How do you usually prepare the frogs?

2.2 Au restaurant / hotel

2.2.1 Do you have frog dishes on the main menu?

2.2.2 How many different dishes do you offer?

2.2.3 What are the different dishes? How do you prepare the frogs?

2.2.4 For how much do you offer a dish of frogs / frog legs?

2.2.5 Which customers do most often order frog dishes?
1. European **2.** Nigerians **3.** Other African Nationality
4. Asian **5.** American

3. Collecting oneself

3.1 From which environment / habitat do the frogs get collected (if more than one place, which quantity is caught at which place (proportionally)?)
1. Pond (permanent) **2.** Pond (temporary) **3.** River **4.** Reservoir
5. Other places:………………………

3.2 During which season of the year do you capture frogs?
1. Dry season **2.** Rainy season **3.** All year round

3.3 Is there a time period when it is forbidden to catch frogs?
If yes, reason:………………………………………………

3.4 At which time of the day do you capture the frogs?
1. Early morning **2.** Midday **3.** Evening **4.** All day round **5.** Night

3.5 Method of collection (if more than one list by importance)
1. Using hands **2.** With a fishing net **3.** With hooks
4. with a basket trap
5. Other:……………..

3.6 How many frogs are you able to collect at once using this method?

3.7 And how many frogs do you usually catch per day/week/month?

3.8 Who is able / is allowed to collect frogs?
*(*Sex, Age, Ethnic, Social Status, Other)

3.9. How often do you consume frogs?

3.10. How many frogs do you usually consume by yourself or in your family?

3.11. Which are the parts you consume?
1. Legs **2.** Trunk without head **3.** Whole frog

3.12. If not the whole body what do you do with the rest?

3.13. How do you usually prepare the frogs?

Appendix 2. Geographical coordinates and locations of the tadpole species found in Burkina Faso (GA: Ganzourghou, GO: Gourma, D: disturbed area, UD: undisturbed area).

Pond ID	Latitude	Longitude	Location	*Afrixalus* spp.	*A. vittiger*	*A. weidholzi*	*Amietophrynus* spp.
PVM1	12°18,666'N	0°52,055'W	GA_D				
PVM2	12°19,659'N	0°50,760'W	GA_D				
PVM3	12°20,635'N	0°47,914'W	GA_D				
PVM4	12°20,705'N	0°47,894'W	GA_D				
PVM5	12°19,351'N	0°51,285'W	GA_D				
PVM6	12°21,198'N	0°45,213'W	GA_D				
PVM7	12°21,305'N	0°44,681'W	GA_D				
PVM8	12°21,702'N	0°42,647'W	GA_D				
PVM9	12°20,952'N	0°42,933'W	GA_D				X
PVM10	12°21,511'N	0°43,124'W	GA_D				
PVM11	12°21,269'N	0°44,811'W	GA_D				
PVM12	12°17,829'N	0°51,690'W	GA_D				
PVM13	12°17,699'N	0°52,037'W	GA_D				
PVM14	12°16,399'N	0°50,247'W	GA_D				
PVM15	12°16,417'N	0°49,874'W	GA_D				X
PVM16	12°15,999'N	0°49,868'W	GA_D				
PRW4	12°23,393'N	1°04,104'W	GA_UD				X
PRW5	12°23,532'N	1°04,053'W	GA_UD			x	
PRW6	12°23,665'N	1°03,909'W	GA_UD				
PRW7	12°23,825'N	1°03,786'W	GA_UD				
PRW8	12°23,984'N	1°03,596'W	GA_UD				
PRW9	12°23,529'N	1°03,957'W	GA_UD	X	x		
PRW10	12°23,592'N	1°03,878'W	GA_UD				
PRW11	12°23,767'N	1°03,659'W	GA_UD				
PRW12	12°24,347'N	1°02,648'W	GA_UD	X			
PRW13	12°24,342'N	1°02,812'W	GA_UD				
PRW14	12°24,275'N	1°03,074'W	GA_UD				
PRW15	12°22,076'N	1°01,222'W	GA_UD				
PRW16	12°22,349'N	1°01,220'W	GA_UD				
PRW17	12°23,138'N	1°01,171'W	GA_UD				
PRW18	12°23,318'N	1°00,594'W	GA_UD				
PVF1	11°51,202'N	0°26,707'E	GO_D				
PVF2	11°51,590'N	0°26,660'E	GO_D				
PVF3	11°51,538'N	0°26,577'E	GO_D				
PVF4	11°51,914'N	0°25,774'E	GO_D				
PVF5	11°55,737'N	0°23,906'E	GO_D				
PVF6	11°55,758'N	0°23,947'E	GO_D				X
PVF7	12°00,798'N	0°01,523'W	GO_D				
PVF8	12°00,743'N	0°01,707'W	GO_D				
PVF9	12°00,679'N	0°02,136'W	GO_D				
PVF10	12°02,957'N	0°02,796'W	GO_D				
PVF11	12°04,974'N	0°26,467'E	GO_D				
PVF12	12°05,487'N	0°27,027'E	GO_D				
PVF13	11°47,293'N	0°26,679'E	GO_D				
PVF14	11°47,549'N	0°26,206'E	GO_D				
PVF15	11°47,693'N	0°26,059'E	GO_D				
PVF16	11°48,537'N	0°24,146'E	GO_D				
PVF17	11°49,014'N	0°24,105'E	GO_D				
PRP1	11°38,643'N	0°31,263'E	GO_UD				
PRP2	11°38,200'N	0°31,380'E	GO_UD				
PRP3	11°38,452'N	0°31,505'E	GO_UD		X		
PRP4	11°39,003'N	0°31,592'E	GO_UD				
PRP5	11°39,185'N	0°31,625'E	GO_UD		X	X	
PRP6	11°39,136'N	0°31,421'E	GO_UD		x		
PRP7	11°37,642'N	0°32,395'E	GO_UD				X
PRP8	11°37,366'N	0°31,462'E	GO_UD				
PRP9	11°37,239'N	0°31,134'E	GO_UD				
PRP10	11°39,329'N	0°31,183'E	GO_UD				
PRP11	11°39,791'N	0°32,438'E	GO_UD				
PRP12	11°39,354'N	0°32,180'E	GO_UD	x		x	x
PRP13	11°39,188'N	0°31,732'E	GO_UD				
PRP14	11°39,076'N	0°31,752'E	GO_UD				
PRP15	11°37,041'N	0°31,971'E	GO_UD				

Appendix 2. continued

Pond ID	Latitude	Longitude	Location	*Amnirana galamensis*	*Hemisus marmoratus*	*Hilde-brandtia ornata*	*Hoplo-batrachus occipitalis*
PVM1	12°18,666'N	0°52,055'W	GA_D		X		
PVM2	12°19,659'N	0°50,760'W	GA_D		X		
PVM3	12°20,635'N	0°47,914'W	GA_D		X		
PVM4	12°20,705'N	0°47,894'W	GA_D				
PVM5	12°19,351'N	0°51,285'W	GA_D			X	
PVM6	12°21,198'N	0°45,213'W	GA_D				
PVM7	12°21,305'N	0°44,681'W	GA_D				
PVM8	12°21,702'N	0°42,647'W	GA_D				
PVM9	12°20,952'N	0°42,933'W	GA_D				
PVM10	12°21,511'N	0°43,124'W	GA_D		X		
PVM11	12°21,269'N	0°44,811'W	GA_D				
PVM12	12°17,829'N	0°51,690'W	GA_D				
PVM13	12°17,699'N	0°52,037'W	GA_D	X			X
PVM14	12°16,399'N	0°50,247'W	GA_D		X		
PVM15	12°16,417'N	0°49,874'W	GA_D				
PVM16	12°15,999'N	0°49,868'W	GA_D		X		
PRW4	12°23,393'N	1°04,104'W	GA_UD				X
PRW5	12°23,532'N	1°04,053'W	GA_UD				
PRW6	12°23,665'N	1°03,909'W	GA_UD	x			
PRW7	12°23,825'N	1°03,786'W	GA_UD				X
PRW8	12°23,984'N	1°03,596'W	GA_UD				
PRW9	12°23,529'N	1°03,957'W	GA_UD				
PRW10	12°23,592'N	1°03,878'W	GA_UD				
PRW11	12°23,767'N	1°03,659'W	GA_UD				
PRW12	12°24,347'N	1°02,648'W	GA_UD				X
PRW13	12°24,342'N	1°02,812'W	GA_UD				X
PRW14	12°24,275'N	1°03,074'W	GA_UD	X			
PRW15	12°22,076'N	1°01,222'W	GA_UD				
PRW16	12°22,349'N	1°01,220'W	GA_UD				
PRW17	12°23,138'N	1°01,171'W	GA_UD			x	X
PRW18	12°23,318'N	1°00,594'W	GA_UD				
PVF1	11°51,202'N	0°26,707'E	GO_D		X		
PVF2	11°51,590'N	0°26,660'E	GO_D		X		
PVF3	11°51,538'N	0°26,577'E	GO_D		X		
PVF4	11°51,914'N	0°25,774'E	GO_D		X		
PVF5	11°55,737'N	0°23,906'E	GO_D				
PVF6	11°55,758'N	0°23,947'E	GO_D				
PVF7	12°00,798'N	0°01,523'W	GO_D		X		
PVF8	12°00,743'N	0°01,707'W	GO_D		X		
PVF9	12°00,679'N	0°02,136'W	GO_D				X
PVF10	12°02,957'N	0°02,796'W	GO_D		X		
PVF11	12°04,974'N	0°26,467'E	GO_D		X		
PVF12	12°05,487'N	0°27,027'E	GO_D		X		
PVF13	11°47,293'N	0°26,679'E	GO_D		X		
PVF14	11°47,549'N	0°26,206'E	GO_D				
PVF15	11°47,693'N	0°26,059'E	GO_D		X		
PVF16	11°48,537'N	0°24,146'E	GO_D		X		
PVF17	11°49,014'N	0°24,105'E	GO_D		X		
PRP1	11°38,643'N	0°31,263'E	GO_UD	x	X		
PRP2	11°38,200'N	0°31,380'E	GO_UD				
PRP3	11°38,452'N	0°31,505'E	GO_UD		X		
PRP4	11°39,003'N	0°31,592'E	GO_UD		X		
PRP5	11°39,185'N	0°31,625'E	GO_UD		X		
PRP6	11°39,136'N	0°31,421'E	GO_UD		X		
PRP7	11°37,642'N	0°32,395'E	GO_UD				
PRP8	11°37,366'N	0°31,462'E	GO_UD		X		
PRP9	11°37,239'N	0°31,134'E	GO_UD				
PRP10	11°39,329'N	0°31,183'E	GO_UD		X		
PRP11	11°39,791'N	0°32,438'E	GO_UD				
PRP12	11°39,354'N	0°32,180'E	GO_UD		X		
PRP13	11°39,188'N	0°31,732'E	GO_UD		X		
PRP14	11°39,076'N	0°31,752'E	GO_UD		X		
PRP15	11°37,041'N	0°31,971'E	GO_UD				

Appendix 2. continued

Pond ID	Latitude	Longitude	Location	*Hyperolius nitidulus*	*H. nasutus*	*Kassina* spp.	*Leptopelis* spp.
PVM1	12°18,666'N	0°52,055'W	GA_D			X	
PVM2	12°19,659'N	0°50,760'W	GA_D			X	
PVM3	12°20,635'N	0°47,914'W	GA_D				
PVM4	12°20,705’N	0°47,894'W	GA_D				
PVM5	12°19,351'N	0°51,285'W	GA_D			X	
PVM6	12°21,198'N	0°45,213'W	GA_D			X	
PVM7	12°21,305'N	0°44,681'W	GA_D			X	
PVM8	12°21,702'N	0°42,647'W	GA_D			X	
PVM9	12°20,952'N	0°42,933'W	GA_D				X
PVM10	12°21,511'N	0°43,124'W	GA_D			X	
PVM11	12°21,269'N	0°44,811'W	GA_D			X	X
PVM12	12°17,829'N	0°51,690'W	GA_D	X		X	
PVM13	12°17,699'N	0°52,037'W	GA_D			X	
PVM14	12°16,399'N	0°50,247'W	GA_D			X	
PVM15	12°16,417'N	0°49,874'W	GA_D			X	
PVM16	12°15,999'N	0°49,868'W	GA_D			X	
PRW4	12°23,393'N	1°04,104'W	GA_UD				
PRW5	12°23,532'N	1°04,053'W	GA_UD			X	
PRW6	12°23,665'N	1°03,909'W	GA_UD			X	X
PRW7	12°23,825'N	1°03,786'W	GA_UD			X	X
PRW8	12°23,984'N	1°03,596'W	GA_UD			X	
PRW9	12°23,529'N	1°03,957'W	GA_UD	X		X	
PRW10	12°23,592'N	1°03,878'W	GA_UD			X	
PRW11	12°23,767'N	1°03,659'W	GA_UD				X
PRW12	12°24,347'N	1°02,648'W	GA_UD			X	X
PRW13	12°24,342'N	1°02,812'W	GA_UD			X	
PRW14	12°24,275'N	1°03,074'W	GA_UD			X	X
PRW15	12°22,076'N	1°01,222'W	GA_UD			X	
PRW16	12°22,349'N	1°01,220'W	GA_UD			X	
PRW17	12°23,138'N	1°01,171'W	GA_UD			X	
PRW18	12°23,318'N	1°00,594'W	GA_UD			X	X
PVF1	11°51,202'N	0°26,707'E	GO_D			X	
PVF2	11°51,590'N	0°26,660'E	GO_D			X	
PVF3	11°51,538'N	0°26,577'E	GO_D			X	
PVF4	11°51,914'N	0°25,774'E	GO_D				
PVF5	11°55,737'N	0°23,906'E	GO_D			X	
PVF6	11°55,758'N	0°23,947'E	GO_D			X	
PVF7	12°00,798'N	0°01,523'W	GO_D			X	
PVF8	12°00,743'N	0°01,707'W	GO_D			X	
PVF9	12°00,679'N	0°02,136'W	GO_D			X	
PVF10	12°02,957'N	0°02,796'W	GO_D				
PVF11	12°04,974'N	0°26,467'E	GO_D			X	
PVF12	12°05,487'N	0°27,027'E	GO_D			X	
PVF13	11°47,293'N	0°26,679'E	GO_D			X	
PVF14	11°47,549'N	0°26,206'E	GO_D			X	
PVF15	11°47,693'N	0°26,059'E	GO_D			X	
PVF16	11°48,537'N	0°24,146'E	GO_D			X	
PVF17	11°49,014'N	0°24,105'E	GO_D				
PRP1	11°38,643'N	0°31,263'E	GO_UD			x	
PRP2	11°38,200'N	0°31,380'E	GO_UD			X	
PRP3	11°38,452'N	0°31,505'E	GO_UD	X	X	X	
PRP4	11°39,003’N	0°31,592'E	GO_UD			X	
PRP5	11°39,185'N	0°31,625'E	GO_UD	X	X	X	
PRP6	11°39,136'N	0°31,421'E	GO_UD			X	
PRP7	11°37,642'N	0°32,395'E	GO_UD	X		X	
PRP8	11°37,366'N	0°31,462'E	GO_UD			X	
PRP9	11°37,239'N	0°31,134'E	GO_UD			X	
PRP10	11°39,329'N	0°31,183'E	GO_UD			X	
PRP11	11°39,791'N	0°32,438'E	GO_UD			X	
PRP12	11°39,354'N	0°32,180'E	GO_UD	X	x	X	
PRP13	11°39,188'N	0°31,732'E	GO_UD				
PRP14	11°39,076'N	0°31,752'E	GO_UD			X	
PRP15	11°37,041'N	0°31,971'E	GO_UD			X	

Appendix 2. continued

Pond ID	Latitude	Longitude	Location	*L. viridis*	*Phryno-batrachus* spp.	*P. latifrons*	*P. francisci*
PVM1	12°18,666'N	0°52,055'W	GA_D	X			
PVM2	12°19,659'N	0°50,760'W	GA_D				
PVM3	12°20,635'N	0°47,914'W	GA_D		X	X	
PVM4	12°20,705'N	0°47,894'W	GA_D			X	X
PVM5	12°19,351'N	0°51,285'W	GA_D		X	X	
PVM6	12°21,198'N	0°45,213'W	GA_D				
PVM7	12°21,305'N	0°44,681'W	GA_D				
PVM8	12°21,702'N	0°42,647'W	GA_D				
PVM9	12°20,952'N	0°42,933'W	GA_D				
PVM10	12°21,511'N	0°43,124'W	GA_D				
PVM11	12°21,269'N	0°44,811'W	GA_D	X			
PVM12	12°17,829'N	0°51,690'W	GA_D	X	X	X	
PVM13	12°17,699'N	0°52,037'W	GA_D		X	X	
PVM14	12°16,399'N	0°50,247'W	GA_D				
PVM15	12°16,417'N	0°49,874'W	GA_D				
PVM16	12°15,999'N	0°49,868'W	GA_D				
PRW4	12°23,393'N	1°04,104'W	GA_UD				
PRW5	12°23,532'N	1°04,053'W	GA_UD	X	X	X	
PRW6	12°23,665'N	1°03,909'W	GA_UD	X	X		
PRW7	12°23,825'N	1°03,786'W	GA_UD	X			
PRW8	12°23,984'N	1°03,596'W	GA_UD	X		X	
PRW9	12°23,529'N	1°03,957'W	GA_UD	X	X	X	X
PRW10	12°23,592'N	1°03,878'W	GA_UD	X	X	X	
PRW11	12°23,767'N	1°03,659'W	GA_UD		X		
PRW12	12°24,347'N	1°02,648'W	GA_UD	X			
PRW13	12°24,342'N	1°02,812'W	GA_UD	X		X	
PRW14	12°24,275'N	1°03,074'W	GA_UD				
PRW15	12°22,076'N	1°01,222'W	GA_UD	X			X
PRW16	12°22,349'N	1°01,220'W	GA_UD	X		X	
PRW17	12°23,138'N	1°01,171'W	GA_UD	X		X	
PRW18	12°23,318'N	1°00,594'W	GA_UD	X		X	
PVF1	11°51,202'N	0°26,707'E	GO_D				
PVF2	11°51,590'N	0°26,660'E	GO_D			X	
PVF3	11°51,538'N	0°26,577'E	GO_D				
PVF4	11°51,914'N	0°25,774'E	GO_D				X
PVF5	11°55,737'N	0°23,906'E	GO_D				
PVF6	11°55,758'N	0°23,947'E	GO_D				
PVF7	12°00,798'N	0°01,523'W	GO_D				
PVF8	12°00,743'N	0°01,707'W	GO_D				
PVF9	12°00,679'N	0°02,136'W	GO_D				
PVF10	12°02,957'N	0°02,796'W	GO_D		X		
PVF11	12°04,974'N	0°26,467'E	GO_D				
PVF12	12°05,487'N	0°27,027'E	GO_D		X		
PVF13	11°47,293'N	0°26,679'E	GO_D			X	
PVF14	11°47,549'N	0°26,206'E	GO_D				
PVF15	11°47,693'N	0°26,059'E	GO_D				
PVF16	11°48,537'N	0°24,146'E	GO_D				
PVF17	11°49,014'N	0°24,105'E	GO_D				
PRP1	11°38,643'N	0°31,263'E	GO_UD	X		X	
PRP2	11°38,200'N	0°31,380'E	GO_UD	X			
PRP3	11°38,452'N	0°31,505'E	GO_UD		X		
PRP4	11°39,003'N	0°31,592'E	GO_UD			X	
PRP5	11°39,185'N	0°31,625'E	GO_UD				
PRP6	11°39,136'N	0°31,421'E	GO_UD	x			
PRP7	11°37,642'N	0°32,395'E	GO_UD				
PRP8	11°37,366'N	0°31,462'E	GO_UD				
PRP9	11°37,239'N	0°31,134'E	GO_UD	X			
PRP10	11°39,329'N	0°31,183'E	GO_UD	X	X		
PRP11	11°39,791'N	0°32,438'E	GO_UD	X			
PRP12	11°39,354'N	0°32,180'E	GO_UD		x	x	
PRP13	11°39,188'N	0°31,732'E	GO_UD	X			
PRP14	11°39,076'N	0°31,752'E	GO_UD	X			
PRP15	11°37,041'N	0°31,971'E	GO_UD	X			

Appendix 2. continued

Pond ID	Latitude	Longitude	Location	*P. natalensis*	*Phryno-mantis microps*	*Ptychadena* spp.	*P. bibroni*
PVM1	12°18,666'N	0°52,055'W	GA_D				
PVM2	12°19,659'N	0°50,760'W	GA_D		X		
PVM3	12°20,635'N	0°47,914'W	GA_D			X	X
PVM4	12°20,705'N	0°47,894'W	GA_D			X	
PVM5	12°19,351'N	0°51,285'W	GA_D		X	X	
PVM6	12°21,198'N	0°45,213'W	GA_D		X		
PVM7	12°21,305'N	0°44,681'W	GA_D			X	
PVM8	12°21,702'N	0°42,647'W	GA_D				
PVM9	12°20,952'N	0°42,933'W	GA_D				
PVM10	12°21,511'N	0°43,124'W	GA_D			X	
PVM11	12°21,269'N	0°44,811'W	GA_D			X	
PVM12	12°17,829'N	0°51,690'W	GA_D		X	X	X
PVM13	12°17,699'N	0°52,037'W	GA_D				
PVM14	12°16,399'N	0°50,247'W	GA_D				
PVM15	12°16,417'N	0°49,874'W	GA_D		X		
PVM16	12°15,999'N	0°49,868'W	GA_D				
PRW4	12°23,393'N	1°04,104'W	GA_UD				X
PRW5	12°23,532'N	1°04,053'W	GA_UD			X	
PRW6	12°23,665'N	1°03,909'W	GA_UD		X	X	
PRW7	12°23,825'N	1°03,786'W	GA_UD				
PRW8	12°23,984'N	1°03,596'W	GA_UD		X		X
PRW9	12°23,529'N	1°03,957'W	GA_UD				X
PRW10	12°23,592'N	1°03,878'W	GA_UD			X	X
PRW11	12°23,767'N	1°03,659'W	GA_UD				
PRW12	12°24,347'N	1°02,648'W	GA_UD				
PRW13	12°24,342'N	1°02,812'W	GA_UD		X	X	X
PRW14	12°24,275'N	1°03,074'W	GA_UD			X	X
PRW15	12°22,076'N	1°01,222'W	GA_UD		X	X	
PRW16	12°22,349'N	1°01,220'W	GA_UD			X	
PRW17	12°23,138'N	1°01,171'W	GA_UD			X	
PRW18	12°23,318'N	1°00,594'W	GA_UD				
PVF1	11°51,202'N	0°26,707'E	GO_D		X		
PVF2	11°51,590'N	0°26,660'E	GO_D		X		
PVF3	11°51,538'N	0°26,577'E	GO_D				
PVF4	11°51,914'N	0°25,774'E	GO_D				
PVF5	11°55,737'N	0°23,906'E	GO_D				
PVF6	11°55,758'N	0°23,947'E	GO_D				
PVF7	12°00,798'N	0°01,523'W	GO_D				
PVF8	12°00,743'N	0°01,707'W	GO_D				
PVF9	12°00,679'N	0°02,136'W	GO_D				
PVF10	12°02,957'N	0°02,796'W	GO_D		X		
PVF11	12°04,974'N	0°26,467'E	GO_D		X	X	x
PVF12	12°05,487'N	0°27,027'E	GO_D		X	X	
PVF13	11°47,293'N	0°26,679'E	GO_D	x			
PVF14	11°47,549'N	0°26,206'E	GO_D				
PVF15	11°47,693'N	0°26,059'E	GO_D				
PVF16	11°48,537'N	0°24,146'E	GO_D				
PVF17	11°49,014'N	0°24,105'E	GO_D				
PRP1	11°38,643'N	0°31,263'E	GO_UD		X		
PRP2	11°38,200'N	0°31,380'E	GO_UD			X	
PRP3	11°38,452'N	0°31,505'E	GO_UD		X		
PRP4	11°39,003'N	0°31,592'E	GO_UD				
PRP5	11°39,185'N	0°31,625'E	GO_UD				
PRP6	11°39,136'N	0°31,421'E	GO_UD				
PRP7	11°37,642'N	0°32,395'E	GO_UD			x	
PRP8	11°37,366'N	0°31,462'E	GO_UD				
PRP9	11°37,239'N	0°31,134'E	GO_UD				
PRP10	11°39,329'N	0°31,183'E	GO_UD				
PRP11	11°39,791'N	0°32,438'E	GO_UD				
PRP12	11°39,354'N	0°32,180'E	GO_UD				
PRP13	11°39,188'N	0°31,732'E	GO_UD				
PRP14	11°39,076'N	0°31,752'E	GO_UD				
PRP15	11°37,041'N	0°31,971'E	GO_UD				

Appendix 2. continued

Pond ID	Latitude	Longitude	Location	*P. oxyrhynchus*	*P. pumilio*	*P. tellini*	*P. tournieri*
PVM1	12°18,666'N	0°52,055'W	GA_D				
PVM2	12°19,659'N	0°50,760'W	GA_D		X		
PVM3	12°20,635'N	0°47,914'W	GA_D				
PVM4	12°20,705'N	0°47,894'W	GA_D				
PVM5	12°19,351'N	0°51,285'W	GA_D				
PVM6	12°21,198'N	0°45,213'W	GA_D				
PVM7	12°21,305'N	0°44,681'W	GA_D		X		
PVM8	12°21,702'N	0°42,647'W	GA_D				
PVM9	12°20,952'N	0°42,933'W	GA_D				
PVM10	12°21,511'N	0°43,124'W	GA_D				
PVM11	12°21,269'N	0°44,811'W	GA_D				
PVM12	12°17,829'N	0°51,690'W	GA_D		X		
PVM13	12°17,699'N	0°52,037'W	GA_D			X	
PVM14	12°16,399'N	0°50,247'W	GA_D				
PVM15	12°16,417'N	0°49,874'W	GA_D				
PVM16	12°15,999'N	0°49,868'W	GA_D				
PRW4	12°23,393'N	1°04,104'W	GA_UD				
PRW5	12°23,532'N	1°04,053'W	GA_UD				
PRW6	12°23,665'N	1°03,909'W	GA_UD		X		X
PRW7	12°23,825'N	1°03,786'W	GA_UD				X
PRW8	12°23,984'N	1°03,596'W	GA_UD				X
PRW9	12°23,529'N	1°03,957'W	GA_UD				X
PRW10	12°23,592'N	1°03,878'W	GA_UD				X
PRW11	12°23,767'N	1°03,659'W	GA_UD				
PRW12	12°24,347'N	1°02,648'W	GA_UD		X	X	X
PRW13	12°24,342'N	1°02,812'W	GA_UD				
PRW14	12°24,275'N	1°03,074'W	GA_UD				X
PRW15	12°22,076'N	1°01,222'W	GA_UD			X	X
PRW16	12°22,349'N	1°01,220'W	GA_UD			X	
PRW17	12°23,138'N	1°01,171'W	GA_UD			X	X
PRW18	12°23,318'N	1°00,594'W	GA_UD			X	
PVF1	11°51,202'N	0°26,707'E	GO_D				
PVF2	11°51,590'N	0°26,660'E	GO_D				
PVF3	11°51,538'N	0°26,577'E	GO_D				
PVF4	11°51,914'N	0°25,774'E	GO_D				
PVF5	11°55,737'N	0°23,906'E	GO_D				
PVF6	11°55,758'N	0°23,947'E	GO_D				
PVF7	12°00,798'N	0°01,523'W	GO_D				
PVF8	12°00,743'N	0°01,707'W	GO_D				
PVF9	12°00,679'N	0°02,136'W	GO_D				
PVF10	12°02,957'N	0°02,796'W	GO_D			X	
PVF11	12°04,974'N	0°26,467'E	GO_D		x	X	X
PVF12	12°05,487'N	0°27,027'E	GO_D				
PVF13	11°47,293'N	0°26,679'E	GO_D				
PVF14	11°47,549'N	0°26,206'E	GO_D				
PVF15	11°47,693'N	0°26,059'E	GO_D				
PVF16	11°48,537'N	0°24,146'E	GO_D				
PVF17	11°49,014'N	0°24,105'E	GO_D				
PRP1	11°38,643'N	0°31,263'E	GO_UD				
PRP2	11°38,200'N	0°31,380'E	GO_UD				
PRP3	11°38,452'N	0°31,505'E	GO_UD				
PRP4	11°39,003'N	0°31,592'E	GO_UD				
PRP5	11°39,185'N	0°31,625'E	GO_UD				
PRP6	11°39,136'N	0°31,421'E	GO_UD				X
PRP7	11°37,642'N	0°32,395'E	GO_UD				
PRP8	11°37,366'N	0°31,462'E	GO_UD	x			
PRP9	11°37,239'N	0°31,134'E	GO_UD				
PRP10	11°39,329'N	0°31,183'E	GO_UD				
PRP11	11°39,791'N	0°32,438'E	GO_UD				
PRP12	11°39,354'N	0°32,180'E	GO_UD				
PRP13	11°39,188'N	0°31,732'E	GO_UD				
PRP14	11°39,076'N	0°31,752'E	GO_UD				
PRP15	11°37,041'N	0°31,971'E	GO_UD				

Appendix 2. continued

Pond ID	Latitude	Longitude	Location	*P. trinodis*	*Pyxicephalus edulis*	*Xenopus muelleri*
PVM1	12°18,666'N	0°52,055'W	GA_D			X
PVM2	12°19,659'N	0°50,760'W	GA_D			X
PVM3	12°20,635'N	0°47,914'W	GA_D			
PVM4	12°20,705'N	0°47,894'W	GA_D			
PVM5	12°19,351'N	0°51,285'W	GA_D			
PVM6	12°21,198'N	0°45,213'W	GA_D			
PVM7	12°21,305'N	0°44,681'W	GA_D			
PVM8	12°21,702'N	0°42,647'W	GA_D			
PVM9	12°20,952'N	0°42,933'W	GA_D			
PVM10	12°21,511'N	0°43,124'W	GA_D			
PVM11	12°21,269'N	0°44,811'W	GA_D			
PVM12	12°17,829'N	0°51,690'W	GA_D			
PVM13	12°17,699'N	0°52,037'W	GA_D			
PVM14	12°16,399'N	0°50,247'W	GA_D			X
PVM15	12°16,417'N	0°49,874'W	GA_D			X
PVM16	12°15,999'N	0°49,868'W	GA_D			X
PRW4	12°23,393'N	1°04,104'W	GA_UD			
PRW5	12°23,532'N	1°04,053'W	GA_UD			
PRW6	12°23,665'N	1°03,909'W	GA_UD			
PRW7	12°23,825'N	1°03,786'W	GA_UD			
PRW8	12°23,984'N	1°03,596'W	GA_UD			
PRW9	12°23,529'N	1°03,957'W	GA_UD			
PRW10	12°23,592'N	1°03,878'W	GA_UD			
PRW11	12°23,767'N	1°03,659'W	GA_UD			
PRW12	12°24,347'N	1°02,648'W	GA_UD	X		
PRW13	12°24,342'N	1°02,812'W	GA_UD			
PRW14	12°24,275'N	1°03,074'W	GA_UD			
PRW15	12°22,076'N	1°01,222'W	GA_UD			
PRW16	12°22,349'N	1°01,220'W	GA_UD			
PRW17	12°23,138'N	1°01,171'W	GA_UD	X		
PRW18	12°23,318'N	1°00,594'W	GA_UD			
PVF1	11°51,202'N	0°26,707'E	GO_D	X		
PVF2	11°51,590'N	0°26,660'E	GO_D		X	
PVF3	11°51,538'N	0°26,577'E	GO_D			
PVF4	11°51,914'N	0°25,774'E	GO_D			
PVF5	11°55,737'N	0°23,906'E	GO_D			
PVF6	11°55,758'N	0°23,947'E	GO_D			
PVF7	12°00,798'N	0°01,523'W	GO_D			X
PVF8	12°00,743'N	0°01,707'W	GO_D			
PVF9	12°00,679'N	0°02,136'W	GO_D			X
PVF10	12°02,957'N	0°02,796'W	GO_D			X
PVF11	12°04,974'N	0°26,467'E	GO_D			
PVF12	12°05,487'N	0°27,027'E	GO_D		X	
PVF13	11°47,293'N	0°26,679'E	GO_D			
PVF14	11°47,549'N	0°26,206'E	GO_D			
PVF15	11°47,693'N	0°26,059'E	GO_D			
PVF16	11°48,537'N	0°24,146'E	GO_D			
PVF17	11°49,014'N	0°24,105'E	GO_D			
PRP1	11°38,643'N	0°31,263'E	GO_UD			
PRP2	11°38,200'N	0°31,380'E	GO_UD			
PRP3	11°38,452'N	0°31,505'E	GO_UD			
PRP4	11°39,003'N	0°31,592'E	GO_UD			
PRP5	11°39,185'N	0°31,625'E	GO_UD			
PRP6	11°39,136'N	0°31,421'E	GO_UD			
PRP7	11°37,642'N	0°32,395'E	GO_UD	x		
PRP8	11°37,366'N	0°31,462'E	GO_UD			
PRP9	11°37,239'N	0°31,134'E	GO_UD			
PRP10	11°39,329'N	0°31,183'E	GO_UD			
PRP11	11°39,791'N	0°32,438'E	GO_UD			
PRP12	11°39,354'N	0°32,180'E	GO_UD			
PRP13	11°39,188'N	0°31,732'E	GO_UD			
PRP14	11°39,076'N	0°31,752'E	GO_UD			
PRP15	11°37,041'N	0°31,971'E	GO_UD			

Appendix 3

Appendix 3. Examples of investigated ponds in Burkina Faso: above left: pond in the undisturbed area in Gourma; down left: pond in the disturbed area in Gourma; above right: pond in undisturbed area in Ganzourghou; down right: pond in the disturbed area in Ganzourghou.

Appendix 4

Appendix 4. above left: *Hoplobatrachus occipitalis*, above right: *Kassina fusca*, middle left: amplectant pair of *Ptychadena bibroni*, middle right: *Phrynomantis microps*, down left: eggs of *P. bibroni*, down right: eggs of *H. occipitalis.*

Appenix 4. continued. Tadpole of *Kassina fusca* is feeding on the waterplant *Ceratophyllum submersum.*

Abbreviations

NMDS	non-metric multidimensional scaling
A.galame	*Amnirana galamensis*
H.marmor	*Hemisus marmoratus*
H.nasutu	*Hyperolius nasutus*
H.nitidu	*Hyperolius nitidulus*
H.occipi	*Hoplobatrachus occipitalis*
Leptopel	*Leptopelis* spp.
Phrynoba	*Phrynobatrachus* spp.
P.microp	*Phrynomantis microps*
P.bibron	*Ptychadena bibroni*
P.pumili	*Ptychadena pumilio*
P.tellin	*Ptychadena tellini*
P.tourni	*Ptychadena tournieri*
P.trinod	*Ptychadena trinodis*
X.muelle	*Xenopus muelleri*
Conducti	electrical conductivity
Veg	estimated vegetation at ponds surface
ST	small plastic tanks
LT	large fiber-glass tanks
DS	development stage

Acknowledgements

My first memory of a frog goes way back in time. I was still not capable to walk but remember being fascinated but also a bit disgusted by the frogs and toads my father used to keep at home at that time. Later, as a child I used to spend a lot of time in the fields and the forest and one of my favourite activities was collecting buckets full of tadpoles and carrying them back home. Who would have known that exactly this activity would have been a major part of my PhD thesis 25 years later?

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Mohneke, M., A.B. Onadeko, M. Hirschfeld and M.-O. Rödel (2010). Dried or fried: amphibians in local and regional food markets in West Africa. Traffic Bulletin 22: 117-128.

List of presentations

Presentation "Unsustainable use of frogs in West Africa?" at the "12th Meeting of the African Amphibian Working Group" in Abomey, Benin (14.-17. August, 2006)

Presentation " Unsustainable use of frogs in West Africa?" at the BIOTA Workshop in Natitingu, Benin (07.-10. October, 2007)

Poster "Unsustainable use of frogs and the ecological consequences in West Africa" at the BIOTA Statusseminar in Kapstadt, Südafrika (28. September – 03. October, 2008)

Presentation "(Un)sustainable use of frogs in West Africa and the resulting effects for the ecosystem" at the Tropentag in Hamburg (06.-08. October, 2009).

Presentation "(Un)sustainable use of frogs: ecological consequences" at the BIOTA Final-Workshop in Ouagadougou, Burkina Faso (25.-28. January, 2010).

Presentation "(Un)sustainable use of frogs: ecological consequences" at the 14th Meeting of the African Amphibian Working Group" in Capetown, South Africa (2nd-4th June, 2010).

Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig angefertigt habe und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Herewith I state that I accomplished the present study independently. I did not use any other resources or references than cited in here.

Berlin, den 10.09.2010

Meike Mohneke