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Declining amphibian populations and possible ecological consequences – a review

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Abstract. Amphibian declines likely result in measurable changes in aquatic and riparian ecosystems. Here, we concentrate on potential consequences of the loss of larval anurans for aquatic ecosystems. In rural savanna regions of West Africa, freshwater ecosystems are essential water resources for humans and cattle. Altering these ecosystems therefore may have important economic and health consequences. Prospective impacts on water chemistry, algae and aquatic invertebrate taxa are highlighted.

Key words. Amphibia, Anura, decline, ecosystem services, freshwater, *Hoplobatrachus occipitalis*, malaria, tadpoles.

Introduction

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 may 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 chytrid fungus, *Batrachochytrium dendrobatides*, which causes chytridiomycosis, are defined as the main causes for their declines (Halliday 2008, Lips et al. 2008, Stuart et al. 2008). Currently one in three amphibian species is threatened with extinction (Stuart et al. 2004, 2008). 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 (Fig. 1), and even predators (Fig. 2). If they are lost directly (e.g. due to agrochemical products) or indirectly (removal of adults), impacts are likely 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 such as mosquito larvae (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 (e.g. 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 abundance, e.g. African puddle frogs, *Phrynobatrachus*, which occur abundantly 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 1,453 *Phrynobatrachus* per hectare. Rödel (1998) counted tadpole (up to 20 species) densities of up to 22.4-30.7 individuals per liter in temporary West African savanna ponds. In a shallow pond, not drying up, he detected more than 1,200 tadpoles per m^2. Declining tadpole numbers will therefore most likely result in altered energy and nutrient cycles, and 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).

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, 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).

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 a short time (Ostroumov 2005), e.g. a maximum filter feeding capacity of 770 ml filtered water per gram per minute was detected for *Xenopus laevis* (Daudin, 1802) 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 themselves on such a diet, tadpoles have to filter a water volume equal to their own body every few minutes (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

(Fig. 3) and their cattle (Fig. 4). Unfortunately and despite their importance for humans, little research has been done on the ecology and function of tropical ponds.

Algal vegetation

Tadpoles' growth rates are often limited by the availability of phytoplankton (Johnson 1991). Conversely, tadpoles' foraging behavior and activity influence 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) showed 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 to persist under the grazing pressure. It is further possible that tadpoles grazing on periphyton may free nutrients for the phytoplankton, and phytoplankton grazers may 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).

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 favor of larval dipterans.

Mosquitoes

Adult, blood-sucking mosquito females often are vectors for human diseases, such as malaria, yellow fever, etc. Hence, knowledge about factors affecting their abundance 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* Macquart, 1838; Culicidae) and tadpoles of the Green toad (*Bufo viridis* Laurenti, 1768; 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 symmetrically. 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 detect-

Fig. 1. Young tadpole of *Kassina fusca* feeding on the water plant *Ceratophyllum submersum*.

Fig. 2. *Hoplobatrachus occipitalis* tadpole pursuing and feeding on a *Ptychadena tellinii* larva.

Fig. 3. Water from temporary ponds is used by the human population in many tropical countries. Water quality in these waters depends on tadpoles' filter-feeding activity. This photo was taken in Burkina Faso.

Fig. 4. Water quality in West African temporary savanna ponds is of large importance to herdsmen and their cattle (Photo: Jörg Szarzynski).

Fig. 5. Mosquito larvae (*Aedes*) feeding on periphyton in a small rock-pool, Pendjari National Park, Benin.

ed that survival rate and adult wing size of *Culex quinquefasciatus* Say, 1823 and *Ochlerotatus australis* (Erichson, 1842) (both Culicidae) 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' feces 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* (Culicidae) and *Culex* larvae are primarily filter feeders, consuming phytoplankton while many *Aedes* (Culicidae) and *Culiseta* mosquito larvae are primarily periphyton feeders (Stav et al. 2005, Matthys et al. 2006, Blaustein & Chase 2007). Hence, anuran and controphic dipteran larvae usually compete with each other and may both alter algal assemblages and biomass.

Some tadpoles do not only compete with mosquito larvae, but act on a higher trophic level as mosquito predators. This especially concerns the very effectively hunting tadpoles of the African *Hoplobatrachus occipitalis* (Günther, 1858). However, these carnivorous tadpoles hunt other tadpoles alike (Fig. 2; 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 (Mohneke et al. 2009), may thus very differently affect mosquito populations.

Human health consequences of 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 threaten 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, treatment costs, lost labor and resulting negative impact of the disease on development, makes malaria a major social and economic burden. In Africa malaria generates annual costs of almost 12 billion US $, slowing the continent's 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. (Culicidae) cause major health problems as well.

Studies have shown that malaria transmission is usually higher in rural than in urban areas (Staedke et al. 2003). There, finding mosquito larvae co-occurring with tadpoles in temporary ponds is more likely (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, bu reducing the size of female mosquitoes, may reduce the insects' disease-carrying potential as smaller mosquitoes have lower fitness and are less likely to transmit significant disease 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 decline, for example by habitat loss or over-exploitation, is hence an urgent research need.

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References

Adolph, E. F. (1931): The size of the body and the size of the environment in the growth of tadpoles. – Biological Bulletin, **61**: 350-375.

Alford, R. A. (1989): Variation in predator phenology affects predator performance and prey community composition. – Ecology, **70**: 206-219.

Barbault, R. (1967): Recherches écologiques dans la savane de Lamto (Côte d'Ivoire): Le cycle annuel de la biomasse des amphibiens et des lézards. – Terre Vie, **3**: 297-318.

Barbault, R. (1972): Les peuplements d'amphibiens des savanes de Lamto (Côte d'Ivoire). – Annales de l'Université d'Abidjan, Sér. E, **5**: 59-142.

Barrera, R., M. Amador & G. G. Clark (2006): Ecological factors influencing *Aedes aegypti* (Diptera: Culicidae) productivity in artificial containers in Salinas, Puerto Rico. – Journal of Medical Entomology, **43**: 484-492.

Blaustein, L & J. M. Chase (2007): Interactions between mosquito larvae and species that share the same trophic level. – Annual Review of Entomology, **52**: 489-507.

Blaustein, L. & J. Margalit (1994): Mosquito larvae (*Culiseta longiareolata*) prey upon and compete with toad tadpoles (*Bufo viridis*). – Journal of Animal Ecology, **63**: 841-850.

Blaustein, L. & J. Margalit (1995): Spatial distributions of *Culiseta longiareolata* (Culicidae, Diptera) and *Bufo viridis* (Amphibia, Bufonidae) among and within desert pools. – Journal of Arid Environments, **29**: 199-211.

Blaustein, L. & J. Margalit (1996): Priority effects in temporary pools: nature and outcome of mosquito larva toad tadpole interactions depend on order of entrance. – Journal of Animal Ecology, **65**: 77-84.

Daily, G. C., S. Alexander, P. R. Ehrlich, L. Goulder, J. Lubchenco, P. A. Matson, H. A. Mooney, S. Postel, S. H. Schneider, D. Tilman, G. M. Woodwell (1997): Ecosystem services: Benefits supplied to human societies by natural ecosystems. – Issues in Ecology, **2**: 1-18.

Dobson, A, D. Lodge, J. Alder, G. S. Cumming, J. Keymer, J. McGlade, H. Mooney, J. A. Rusak, O. Sala, V. Wolters, D. Wall, R. Winfree & M. A. Xenopoulos (2006): Habitat loss, trophic collapse, and the decline of ecosystem services. – Ecology, **87**: 1915-1924.

Ernst, R. & M.-O. Rödel (2006): Community assembly and structure of tropical leaf-litter anurans. – Ecotropica, **12**: 113-129.

Flecker, A. S., B. P. Feifarek & B. W. Taylor (1999): Ecosystem engineering by a tropical tadpole: density-dependent effects on habitat structure and larval growth rates. – Copeia, **1999**: 495-500.

Gardner T. A., E. B. Fitzherbert, R. C. Drewes & T. Caro (2007): Spatial and temporal patterns of abundance diversity of an East African leaf litter amphibian fauna. – Biotropica, **39**: 105-113.

Hagman, M. & R. Shine (2007): Effects of invasive cane toads on Australian mosquitoes: does the dark cloud have a silver lining? – Biological Invasions, **9**: 445-452.

Halliday, T. R. (2008): Why amphibians are important. – International Zoo Year Book, **42**: 1-8.

Heyer, W. R. & M. H.Muedeking (1996): Notes on tadpoles as prey for naiads and turtles. – Journal of the Washington Academy of Science, **66**: 235-239.

Hooper, D. U., F. S. Chapin, III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorei, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeeret & D. A. Wardle (2005): Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. – Ecological Monographs, **75**: 3-35.

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

Johnson, L. M. (1991): Growth and development of larval northern cricket frogs (*Acris crepitans*) in relation to phytoplankton abundance. – Freshwater Biology, **25**: 51-59.

Kiffney, P. M. & J. S. Richardson (2001): Interactions among nutrients, periphyton, and invertebrate and vertebrate (*Ascaphus truei*) grazers in experimental channels. – Copeia, **2001**: 422-429.

Knight, T. M., J. M. Chase, C. W. Goss & J. J. Knight (2004): Effects of interspecific competition, predation, and their interaction on survival and development time of immature *Anopheles quadrimaculatus*. – Journal of Vector Ecology, **29**: 277-284.

Kopp, K., M. Wachlevski & P. C. Eterovick (2006): Environmental complexity reduces tadpole predation by water bugs. – Canadian Journal of Zoology, **84**: 136-140.

Kupferberg, S. (1997): Facilitation of periphyton production by tadpole grazing: functional differences between species. – Freshwater Biology, **37**: 427-439.

Lamberti, G. A., S. V. Gregory, C. P. Hawkins, R. C. Wildman, L. R. Ashkenas, D. M. Denicola (1992): Plant - herbivore interactions in streams near Mount St Helens. – Freshwater Biology, **27**: 237-247.

Lips, K. R., J. Diffendorfer, J. R. Mendelson III & M. W. Sears (2008): Riding the wave: reconciling the roles of disease and climate change in amphibian declines. – Plos Biology, **6**: 441-454.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman & D. A. Wardle (2001): Biodiversity and ecosystem functioning: current knowledge and future challenges. – Science, **294**: 804-808.

Matthys, B., E. K. N. Goran, M. Kone, B. G. Koudou, P. Vounatsou, G. Cisse, A. B. Tschannen, M. Tanner & J. Utzinger (2006): Urban agricultural land use and characterization of mosquito larval habitats in a medium-sized town of Côte d'Ivoire. – Journal of Vector Ecology, **31**: 319-333.

McCollum, S. A. & J. D. Leimberger (1997): Predator-induced morphological changes in an amphibian: predation by dragonflies affects tadpole shape and color. – Oecologia, **109**: 615-621.

McDiarmid, R. W. & R. Altig (1999): Tadpoles – The biology of anuran larvae. – Chicago, Chicago University Press.

McLachlan, A. (1981): Interaction between insect larvae and tadpoles in tropical rain pools. – Ecological Entomology, **6**: 175-182.

Mohneke, M., A. B. Onadeko & M.-O. Rödel (2009): Exploitation of frogs – a review with a focus on West Africa. – Salamandra, **45:** 193-202.

Mokany, A. & R. Shine (2002a): Pond attributes influence competitive interactions between tadpoles and mosquito larvae. – Australian Ecology, **27**: 396-404.

Mokany, A. & R. Shine (2002b): Competition between tadpoles and mosquitoes: the effects of larval density and tadpole size. – Australian Journal of Zoology, **50**: 549-563.

Mokany, A. & R. Shine (2003a): Biological warfare in the garden pond: tadpoles suppress the growth of mosquito larvae. – Ecological Entomology, **28**: 102-108.

Mokany, A. & R. Shine (2003b): Competition between tadpoles and mosquito larvae. – Oecologia, **135**: 615-620.

Osborne, P. L. & A. J. McLachlan (1985): The effect of tadpoles on algal growth in temporary, rain-filled rock pools. – Freshwater Biology, **15**: 77-87.

Ostroumov, S. A. (2005): Some aspects of water filtering activity of filter-feeders. – Hydrobiologia, **542**: 275-286.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky & K. D. Wells (2001): Herpetology. – Upper Saddle River, Prentice-Hall.

Poulin, B., G. Lefebvre, R. Ibanez, C. Jaramillo, C. Hernandez & A. S. Rand (2001): Avian predation upon lizards and frogs in a neotropical forest understorey. – Journal of Tropical Ecology, **17**: 21-40.

Ranvestal, A. W., K. R. Lips, C. M. Pringle, M. R. Whiles & R. J. Bixby (2004): Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. – Freshwater Biology; **49**: 274-285.

Rödel, M.-O. (1998): Kaulquappengesellschaften ephemerer Savannengewässer in Westafrika. – Frankfurt/M., Edition Chimaira.

Rödel, M.-O. (1999): Predation on tadpoles by hatchlings of the freshwater turtle *Pelomedusa subrufa*. – Amphibia-Reptilia, **20**: 173-183.

Rudolf, V. H. W. & M.-O. Rödel (2007): Phenotypic plasticity and optimal timing of metamorphosis under uncertain time constraints. – Evolutionary Ecology, **21**: 121-142.

Sanderson, S. L. & R. Wassersug (1990): Suspension-feeding vertebrates. – Scientific American, **262**: 68-73.

Seale, D. B. (1980): Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. – Ecology, **61**: 1531-1550.

Spieler, M. & K. E. Linsenmair (1998): Migration patterns and diurnal use of shelter in a ranid frog of a West African savannah: a telemetric study. – Amphibia-Reptilia, **19**: 43-64.

Staedke, S. G., E. W. Nottingham, J. Cox, M. R. Kamya, P. J. Rosenthal & G. Dorsey (2003): Proximity to mosquito breeding sites as a risk factor for clinical malaria episodes in an urban cohort of Ugandan children. American Journal of Tropical – Medicine and Hygiene, **69**: 244-246.

Stav, G., L. Blaustein & Y. Margalit (2005): Individual and interactive effects of a predator and controphic species on mosquito populations. – Ecological Applications, **15**: 587-598.

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

Stuart, S. N., M. Hoffmann, J. S. Chanson, N. A. Cox, R. J. Berridge, P. Ramani & B. E. Young (2008): Threatened Amphibians of the World. – Barcelona, Lynx Editions.

Tyler, M. J., R. Wassersug & B. Smith (2007): How frogs and humans interact: influences beyond habitat destruction, epidemics and global warming. – Applied Herpetology, **4**: 1-18.

Toledo, L. F., R. S. Ribeiro & C. F. B. Haddad (2007): Anurans as prey: an exploratory analysis and size relationships between predators and their prey. – Journal of Zoology, **271**: 170-177.

Viertel, B. (1992): Functional response of suspension feeding anuran larvae to different particle sizes at low concentrations (Amphibia). – Hydrobiologia, **234**: 151-173.

Wager, V. A. (1965): The frogs of South Africa. – Capetown, Purnell & Sons.

Whiles, M. R., K. R. Lips, C. M. Pringle, S. S. Kilham, R. J. Bixby, R. Brenes, S. Connelly, J. C. Colon-Gaud, M. Hunte-Brown, A. D. Huryn, C. Monztomery & S. Peterson (2006): The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. – Frontiers in Ecology and the Environment, **4**: 27-34.

Wilbur, H. M. (1997): Experimental ecology of food webs: complex systems in temporary ponds. – Ecology, **78**: 2279-2302.

World Health Organization (2004): Malaria control – progress report on implementation of the plan of action of the Abuja declaration. – World Health Organization, Regional Offices for Africa and Eastern Mediterranean.

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