Phyllomedusa 6(2):83-103, **2007**
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ISSN 1519-1397

REVIEW ARTICLE

Physiology, environmental change, and anuran conservation

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Abstract

Physiology, environmental change, and anuran conservation. This paper reviews diverse ways in which the emerging discipline of conservation physiology may contribute to the conservation of anuran amphibians. We first present a summary of the goals of conservation physiology. Then, we review five specific sources of environmental change that are known to affect anurans: introduced pathogens (highlighting the case of chytridiomycosis) and exotic species, pollutants, habitat fragmentation, and global climate change. We discuss these types of environmental change in the context of how and why altered environments may become stressing to anurans and cause population declines. We also discuss synergism among variables that may worsen the effect of environmental alterations, and emphasize the importance of conservation physiology for Brazilian anurans.

Keywords: Anura, conservation physiology, environmental change, chytridiomycosis, exotic species, pollutants, habitat fragmentation, global climate change.

1. Introduction

Comparative physiology has a long-standing history of collateral contributions to conservation biology, but recently the specific field of conservation physiology has grown to be considered an independent emerging discipline (Wikelski and Cook 2006). An important goal of this new field is to understand the ability of organisms to deal with environmental change, including those resulting from human influence. Although human-induced changes tend to be very rapid and have the potential to affect all organisms, some taxonomic groups are far more susceptible to environmental change than others. Anuran amphibians figure among the most vulnerable taxa, as deduced from current dramatic rates of population and species extinction. The decline of anuran populations and its relationships with ecological change have been the focus of divergence regarding proper actions to be taken (Mendelson *et al.* 2006, Parmesan 2006, Pounds *et al.* 2006a), a debate to which conservation physiology may contribute significantly. In this paper we discuss how physiological studies may bolster the cause of anuran conservation and management.

Received 14 June 2007.
Accepted 21 November 2007.
Distributed December 2007.

2. A synopsis on the goals and principles of conservation physiology

The possible outcomes of noxious environmental change to organisms are local extinction, migration, or adjustment to the new condition (Donnelly 1998, Helmuth *et al.* 2005). Adjustment, in this case, means a modification of behavior or physiology that ameliorates the effect of a stressful change in environmental conditions. Physiological adjustments are often the only mechanism by which organisms facing environmental change can maintain homeostasis, the state of internal equilibrium required for life (Carey 2005, Wikelski and Cooke 2006). The ability to maintain homeostasis through time is intuitively related to the life-time ecological success of organisms exposed to environmental change (McEwen and Wingfield 2003), and is called allostatic capacity (Wikelski and Cooke 2006). The point at which the threshold for stress tolerance of a population is surpassed is known as allostatic overload. This is a valuable concept in conservation physiology because it relates stress to a physiological state more than to the type, magnitude, or time-scale of the stressor (Wikelski and Cooke 2006).

Differences in allostatic capacity result from physiological adjustments occurring at various levels of organization (e.g., individuals, populations, and species) and time scales (Wikelski and Cooke 2006). Within the lifetime of an individual, for example, fully reversible adjustments may occur through the process of acclimatization. Likewise, modifications of physiology, reversible or not, may occur through development and under the influence of the environment, and are associated with the concept of phenotypic plasticity. Finally, adjustments leading to shifts in allostatic capacity may take place across generations in the context of evolutionary processes. Many examples of the importance of these processes exist in the literature. Acclimatization to temperature, for example, seems fundamental for crabs to adjust to global warming (Stillman 2003), and directional changes in the frequency of alleles linked to stress physiology, and attributable to climate change, have been observed in mountain insects (Rank and Dahlhoff 2002). The physiological tolerance of insects to humidity and temperature is related to geographic range, and apparently shifts in association with climatic change (Karban and Strauss 2004).

Three goals of conservation physiology that we believe are of particular importance are 1) to understand the scope and paths through which organisms facing noxious environmental change adjust their physiology to overcome stress (Wikelski and Cooke 2006); 2) to reveal the physiological challenges that affect critical parts of the life cycles of organisms (Helmuth *et al.* 2005); and 3) to evaluate the costs and trade-offs associated with physiological adjustments. These costs may be direct, in the sense that noxious environmental change may either increase the energy requirements of animals or decrease their ability to obtain energy (Carey 2005, Wikelski and Cooke 2006). The cost of maintenance of amphibians, for example, may increase directly as a consequence of temperature shifts (see Section 3.2) or exposure to pollutants (see Section 3.4). Energy expenses may also increase indirectly, for example when environmental change results in increased need for locomotion (Carey 2005, Wikelski and Cooke 2006) (see Section 3.5). Conversely, pathological conditions (Parris *et al.* 2006) or experimental exposition to predators (Skelly 1992) may reduce the inclination for activity in anuran tadpoles. When environmental change downgrades energetic budgets, organisms need to reduce allocation to growth, storage, reproduction or activity (Calow 1991, Brauner *et al.* 1994, Hopkins *et al.* 1997, Rowe *et al.* 1998, Beyers *et al.* 1999, Barbieri *et al.* 2002). Energy, however, is not the only possible price of physiological adjustments. Additional potential costs include phenotypic trade-offs, that is, additional changes that occur in parallel with physiological adjustments, and that result from phenotypic correlations among traits (Angilletta *et al.* 2003, Helmuth *et al.* 2005). Phenotypic correlations may be based in genetic correlations. For example, selection favoring a reduction in the thermal dependency of developmental rate of *Rana sylvatica* results in a concomitant, and apparently unavoidable, thermal dependency of body size (Berven 1982).

Several fields of physiology have made important contributions to conservation, and interested readers should consult the reviews by Carey (2005), Helmuth *et al.* (2005), and Wikelski and Cooke (2006). In summary, endocrinology, ecological physiology, immunology, physiological genomics and other physiological disciplines have provided tools to evaluate stress, illustrate the control and triggers of reproduction, understand the patterns of animal distribution, and to comprehend the effects of physical variables on physiology. Evolutionary physiology has contributed greatly to understanding the factors that modulate and restrict the evolution of physiological traits (Angilletta *et al.* 2002), with concrete links with life-history traits (Sears and Angilletta 2004). Comparative and ecological physiology have helped in the understanding of acclimation, reversible physiological responses by which organism may adjust to environmental change such as global warming (Stillman 2003). The applications of physiology to anuran conservation are clearly many, and it would be beyond the scope of this paper to treat them all. Instead, we highlight in the next sections some scenarios that may interest a broad audience of herpetologists, and that illustrate how physiological studies may contribute to the conservation and management of endangered anuran amphibians.

3. Anurans and environmental change

In this section we focus on five categories of environmental degradation that are particularly important for anuran conservation. First, we focus on human-spread pathogens, specifically chytridiomycosis, the putative causal agent of the decline and extinction of several anuran populations and species (Daszak *et al.* 2001). The second category is global climate change, and the need to understand how anuran physiology would react to changes in mean temperature and thermal variance, and to extreme climatic events. Then, we describe briefly the importance of understanding synergistic effects among environmental variables, focusing on temperature and chytridiomycosis. Subsequently, we move to pollutants, which may become stressors, particularly at early developmental stages. Water pollution may have deleterious effects on anuran egg hatching, perhaps acting synergistically with other factors (Karasov *et al.* 2005). Next, we review habitat fragmentation, and discuss why survival in a fragmented forested environment may be influenced by the ability of individuals to cross gaps. This factor has been recognized as an important attribute for the survival of anuran populations (Zimmerman and Bierregaard 1986, Dale *et al.* 1994) but has received little formal attention. Finally, we center on the physiological and behavioral ability of exotic species to outcompete local species, which is another point of interface between conservation biology and physiology.

3.1. *Chytridiomycosis*

Chytridiomycosis is a disease caused by a fungus, *Batrachochytrium dendrobatidis,* and is, for many scientists, the causal agent explaining local anuran extinction (Berger *et al.* 1998, Collins 2003, Daszak *et al.* 2003, Lips *et al.* 2003a,b, Retallick *et al.* 2004, Lips *et al.* 2005, Woodhams and Alford 2005, Pounds *et al.* 2006a). The decline of anuran populations from chytridiomycosis has become a top issue in conservation biology, one to which investigations in comparative and ecological physiology have much to offer. Anuran species differ in their susceptibility to chytridiomycosis (Berger *et al.* 1998, Lips *et al.* 2003a,b, Retallick *et al.* 2004, Woodhams and Alford 2005, Woodhams *et al.* 2006a), and this variation apparently stems from differences in the immune system (Woodhams *et al.* 2006a). A main immune organ of anurans, generally the first one to enter in contact with *B. dendrobatidis* in the field, is the skin (Carey 2005). Therefore, a step to understand interspecific differences in susceptibility to chytridiomycosis is to perform comparative studies of the morpho-physiology of the anuran skin, and of the ecologically-relevant microbiological properties of its secretions. The anuran skin contains various types of glands, including the granular glands involved in the production of antimicrobial peptides. A large number of anuran-skin peptides and alkaloids (amines) have been characterized (see review in Pukala *et al.* 2006), but few species have been studied, particularly in Neotropical regions. These skin peptides, which vary in type and proportion among species, confer various degrees of protection from pathogens, including *B. dendrobatidis* (Rollins-Smith *et al.* 2002a,b, 2005, Rollins-Smith and Conlon 2005, Woodhams *et al.* 2006a) or bacteria isolated from natural habitats (Ashcroft *et al.* 2007). Further studies will help to understand the mechanisms underlying peptide action (Rollins-Smith *et al.* 2002a,b) and the eventual phylogenetic constraints related to chytridiomycosis vulnerability (Woodhams *et al.* 2006b).

Physiological ecology is relevant in the context of chytridiomycosis because a number of environmental factors that may further increase stress levels, including temperature, intensity of UV-B radiation and concentration of toxic chemicals, influence susceptibility to the disease (Johnson *et al.* 2003). Noxious environmental conditions may increase the chances of infection by depressing the protection derived from skin products (Rollins-Smith *et al.* 2002a,b), and by increasing the concentration of circulating glucocorticoids (Simmaco *et al.* 1997, Matutte *et al.* 2000), stress-related steroid hormones derived from cholesterol that may be harmful when chronically elevated. Immunological depression may also have an indirect, but perhaps important, link with the biotic environmental. This is so because part of the chemicals produced by the anuran skin, alkaloids in particular, are sequestered from dietary sources including ants, beetles, millipedes, and other arthropods (Daly 1995). As a consequence, a depauperate ecological community may constrain the biochemical profile of anuran skin secretions.

3.2. *Global climate change*

The physiological adjustments required of the organisms in response to climate change is a cause of concern among scientists working on systematic groups as diverse as plants (Beardall *et al.* 1998), fish (D'Cruz *et al.* 1998), birds (Wolf 2000), and certainly, amphibians. Ever since the population crash of the Costa Rican golden toad, *Ollotis periglenes,* in 1987, attributed to erratic weather perhaps induced by global warming (Pounds and Crump 1994), herpetologists have been concerned about climate change and anuran conservation. From what we know from physiology, this concern is fully justified. Anurans experience pervasive effects of temperature on their behavioral and physiological function, including the immune system (Beecher and Demas 2004), and may respond to infection using behavioral thermoregulation. Not surprisingly, therefore, the intricate ways by which global climate change may affect anurans include interactions with other major problems such as chytridiomycosis (see next section). It is also essential to keep in mind that global climate change is not a smooth monotonic increase in environmental temperatures, but a complicated pattern in which emerging extreme events are of substantial importance (Marengo 2006, Mitchell *et al.* 2006). Droughts associated with global warming, for example, in combination with other factors such as fungal infections, may have been the cause of populational declines in *Eleutherodactylus* from Puerto Rico (Burrowes *et al.* 2004). Frosts possibly contributed to the decline of anuran communities in the Brazilian Atlantic Forest (Heyer *et al.* 1988; see Section 4), and a reduction of the amount of rain per year possibly caused the anuran population declines observed during long-term studies at the Savannah River Site (SRS) in South Carolina, USA (Daszak *et al.* 2005). It is impossible to prove that these past atypical climatic extremes actually caused the declines, and it would be even more difficult to prove that such extremes were a direct consequence of the global warming phenomenon. However, the data available do suggest that climate extremes may be consequential for anuran populations, and that the likelihood of such events to occur has increased with global warming. Understanding the scope and physiological basis for anuran tolerance to climate extremes seems an imperative issue in the agenda for anuran conservation.

An important concern when discussing the implications of climate change for anuran conservation regards their possibilities for behavioral and physiological adjustment to temperature change. Behavioral responses, such as a shift towards an earlier onset of calling activity during the day, do not compensate for reduced temperature in high-elevation Andean anurans (Navas 1996a). Some temperate anuran species appear to compensate for a warmer climate by shifting the time of year in which the reproductive season occurs (Beebee 1995), but no common trend exists, and a number of species in North-America and Europe have not adjusted reproduction in this manner (Blaustein *et al.* 2001, 2003, Beebee 2002, Corn 2003). In addition, even when present, behavioral adjustments may be insufficient to compensate for the effects of warming. Warmer winters, for example, affect the reproductive output of *Bufo bufo* by decreasing female body condition during hibernation (Reading 2007). Warming may also affect the morphology of anurans, particularly body size. Males of the "*Rana esculenta*" complex (water frogs of Central Europe) exhibit body sizes that are up to 10% larger than those measured in 1963, a period over which indirect measures suggest that temperatures became more moderate. Females, in contrast, exhibited no or contradictory patterns, a finding that illustrates the complexity of temperature effects on anurans (Tryjanowski *et al.* 2006). Because temperature may affect the type and availability of prey items, which in turn relates to growth rates, temperature may also cause indirect effects on anuran adult size (Tryjanowski *et al.* 2006). Overall, physiological, more than behavioral adjustments appear to compensate for climate change in anurans.

Global climate change generates particular risk to species adapted to cool or to extreme environments. Some species from polar or high altitude environments, for example, already show drastic contractions of their natural ranges (Parmesan 2006). Altitude seems to be a factor increasing the risk of anuran population declines, although its possible effects are not simple in pattern (Pounds *et al.* 2006a). An example in which a concrete causative relationship between temperature and physiological stress has been proposed concerns montane salamanders from the Appalachian highlands (*Desmognathus*). These cold-adapted salamanders, perhaps due to evolutionary or physiological constraints, do not exhibit adjustments with respect to the effects of temperature on the cost of maintenance (metabolic rate) along an altitudinal gradient. Although the metabolic rate is temperature dependent between 5 and 15ºC, as expected for amphibians in general, higher temperatures cause a drastic metabolic depression that is evident in tests performed between 15 and 20ºC. This depression is highest in individuals from the lowest elevation site in the study (963 m), suggesting that this species complex is physiologically constrained to high elevations (Bernardo and Spotila 2006).

3.3. *Temperature and chytridiomycosis as an example of synergistic environmental effects*

Some authors defend the idea that global warming is a key factor promoting the action of *B. dendrobatidis* (Pounds *et al.* 2006a, Bosch *et al.* 2007), while admitting that this pathogen, even if present, may not always be a main causative agent of decline (Pounds *et al.* 2006b). Although the available studies show association more than causation, they point to a potential crucial interaction in anuran conservation. Comparative physiology is already helping to elucidate the relationship between chytridiomycosis and temperature. It is clear that the relationships between infectious agents and anuran hosts is influenced by thermoregulatory behaviors and by thermal ecology (Berger *et al.* 1998, Alford and Richards 1999). The varieties of the fungus *B. dendrobatidis* studied so far grow best at moderate temperatures, i.e., slightly above 20ºC (Berger *et al.* 2004, Daszak *et al.* 2003, Burrowes *et al.* 2004, Pounds *et al.* 2006a), so that, global warming leading to increased daily body temperatures may increase the risk of infection of certain populations (Pounds *et al.* 2006a). However, temperatures well above the peak for fungal growth yet moderate for anurans (e.g., 28-30ºC) inhibit or even kill the pathogen and help frogs to fight infection (Woodhams *et al.* 2003, Pounds *et al.* 2006a). Such temperatures can be attained by anurans through thermoregulatory behaviors leading to body temperatures higher than normal. Such thermoregulatory shifts were first reported for small thermophilic lizards (Kluger *et al.* 1975) but are currently known to occur in diverse vertebrate tetrapods including anurans, and to help animals to survive bacterial infection (Myhre *et al.* 1977, Sherman *et al.* 1991, Woodhams *et al.* 2003). Because opportunity for thermoregulation and typical body temperatures vary among anurans, even when comparing syntopic species (Navas 1996b), vulnerability to pathogens may vary as a consequence of differences in patterns of activity and preferred microhabitat. The relevance of thermal ecology to pathogen-host relationships in anurans is illustrated by studies on seasonality and environmental temperatures. During the winter months (Berger *et al.* 2004), or in environments likely to have summer temperatures lower than 30ºC (Drew *et al.* 2006), the incidence of chytridiomycosis in Australian frogs increases. What we conclude is that a comprehensive analysis of microhabitat selection, patterns of activity, and field body temperatures is fundamental to fully understand anuran vulnerability to chytridiomycosis.

3.4. *Pollutants*

Because of its magnitude and ubiquity, a main factor threatening biodiversity in general, and amphibians in particular, is chemical pollution (Koeman 1991, Carey and Bryant 1995, Schiesari *et al.* 2007). The effects of pollutants on organisms in natural environments is the primary subject of ecotoxicology, whereas understanding the mechanisms by which organisms rid themselves of toxic substances is one topic of study in comparative physiology. These two fields meet in ecophysiological approaches focused on conservation biology, aiming to evaluate and predict the environmental risks of pollution contaminants to the environment (Koeman 1991, Stevenson *et al.* 2005). Because of a life-history usually involving aquatic larvae and terrestrial adults, and to a permeable and vascularized skin, amphibians seem particularly prone to uptake pollutants (Donnelly 1998, Maxell 2000, Schiesari *et al.* 2007). Although important caveats have been noted (Beebee and Griffiths 2005), amphibians have become widely recognized as indicators of environmental quality. They are lethally affected by petroleum products (Mahaney 1994), acidification (Rowe *et al.* 1992, Sadinski and Dunson 1992), insecticides (Berrill *et al.* 1993, 1994), and various metals (Freda 1991). Anuran species, however, differ in their ability to tolerate chemical contaminants (Hall and Henry 1992, Bridges and Semlitsch 2000, Rowe *et al.* 2001, Christin *et al.* 2004). These differences relate to the concept of allostatic capacity, and could be better understood using integrative approaches involving comparative physiology and ecotoxicology.

As evident from the discussion in Section 3.3, conservation physiology can contribute to understanding synergistic effects of environmental stressors. Pollutants may increase anuran vulnerability to pathogens, predators, ultraviolet radiation, or climate change (Little *et al.* 2000, Carey *et al.* 2001, Relyea and Millis 2001). One complication is that the effects of pollutants on organisms may be drastic only after chronic exposure. These types of effects, usually termed sublethal, include depressed disease resistance, inhibition of growth and development, decreased reproductive ability, inhibition of predator avoidance behaviors, and increased likelihood of developing morphological abnormalities (Lefcort *et al.* 1998, Maxell 2000, Christin *et al.* 2004, Gurushankara *et al.* 2007). Anuran populations are not exceptional, and may be affected sublethally by progressive accumulation of organic compounds or heavy metals in their tissues (Hall and Mulhern 1984). The accumulation of toxic substances sometimes results in morphological or physiological changes (Calow 1991, Alvarez *et al.* 1995, Rowe *et al.* 1996, 1998), and may affect energetics. In a number of animal species, the sublethal effects of toxic compounds include an increase in metabolic rate (Calow 1991, Hopkins *et al.* 1998, Beyers *et al.* 1999, Naab *et al.* 2001, Barbieri *et al.* 2002), but the effects of contaminants on anuran energetics are not well understood. The concentration of coal-ash-derived pollutants is related to elevated metabolic rates in the bullfrog, *Lithobates catesbeianus* (Rowe *et al.* 1998), but not in *Anaxyrus terrestris* (Rowe *et al.* 2001). As in other examples cited before, the same kind and magnitude of environmental change, in this case pollutant type and concentration, may affect amphibian species in diverse, even contrasting ways (Calow and Sibly 1990, Koeman 1991). A full understanding of the relationship between anuran ecology, physiology, and ecotoxicology requires much additional work and information about the concentration, persistence, and spatio-temporal variation of pollutants in the environment (Davidson *et al.* 2002, Schiesari *et al.* 2007).

Although comparative physiology can help to clarify how anuran populations are affected by pollutants, the biogeographic zones with highest amphibian diversity have been neglected in these types of studies (Schiesari *et al.* 2007). Common contaminants such as organochlorine pesticides disrupt normal endocrine function and lead to reduced oogenesis and reproductive output in *Xenopus laevis* (Pickford and Morris 2003). Pesticides may also disrupt the normal course of steroid hormone production and result in demasculinization and hermaphroditism (Hayes *et al.* 2002, 2003). The threatened California red legged frog (*Rana draytonii*), at some point believed to be mainly affected by global warming, turned out to be particularly sensitive to agrochemicals (Davidson *et al.* 2001). Comparative immunological studies demonstrate that a realistic (i.e., likely to appear in the province of Quebec, Canada) mixture of agricultural pesticides reduce, although in different manners, the efficacy of the immune system of *X. laevis* and *Lithobates pipiens* (Christin *et al.* 2004). A mixture of pesticides used in US cornfields cause similar effects, and are associated with an increase in plasma levels of the stress hormone corticosterone (see note on stress hormones in Section 3.1) (Hayes *et al.* 2006). Comparative physiology has also helped to elucidate mechanisms behind specific pathological conditions of anurans exposed to pollution. For example, exposure to an acidic environment favors the opportunistic infection of the spleen by otherwise non-pathological bacteria, apparently by disrupting the integrity of epithelial barriers that normally prevent migration of intestine bacteria to the blood (Simon *et al.* 2002).

3.5. Habitat fragmentation

A consequence of urban and agricultural development is the transformation of formerly large extensions of continuous habitat into isolated patches of preserved areas (Miller and Cale 2000, Andersen *et al.* 2004, Pinto and Brito 2005). Habitat fragmentation may benefit a number of open-area anurans (Carnaval 2002), for example *Chaunus marinus* and *Scinax ruber*, two species frequently observed on the roads and farms built in the Amazonian forest (Duellman 1999). Local extinction and reduction of species richness, however, is a more common trend in fragmented habitats (Connor and McCoy 1979, Laan and Verboom 1990, Fahrig and Merriam 1994, Zuidema *et al.* 1996, Marsh and Pearman 1997, Vallan 2000, Pineda and Halffter 2004, Drinnan 2005, Funk *et al.* 2005, Bell and Donnelly 2006, Neckel-Oliveira and Gascon 2006). The anuran communities of fragmented habitats normally exhibit a subgroup of the presumed original communities (Ficetola and De Bernardi 2004, Bell and Donnelly 2006, Woinarski *et al.* 2006), and why this is so is a fundamental question for anuran conservation.

The effects of habitat fragmentation on anuran communities probably has three main groups of causes. The first one is reduced arthropod diversity (Maleque *et al.* 2006), and the possibility that an impoverished diet makes anuran more fragile or susceptible to infection (see Section 3.1). The second group of causes relates to reproduction, a topic mentioned already in the discussion of pollution and global climate change, and that we will treat in the next paragraph from the perspective of ability to reach breeding grounds. The third group of causes refers to the pool of changes in the magnitude and variance of physical variables that characterize habitat fragmentation. Habitat fragments are, from many points of view, poorer environments than the original habitats, and are also more prone to extremes in the sense that a number of relevant physical characteristics become less predictable. Compared to the core of the forest, for example, the edges of forest patches are more exposed to wind, solar radiation, thermal variance and dehydration. Not only do these characteristics reduce the effective habitat area available for forest-adapted organisms (Saunders *et al.* 1991, Murcia 1995), but habitat remnants are more exposed to agrochemical inputs, influence from logging, livestock grazing, and induced fire (Turner 1996). The ability of anuran species to tolerate the novel physical regimes brought about by fragmentation relates to the concept of allostatic capacity cited in Section 2 and applies to all developmental phases, from eggs to adults. Although tadpoles of some species tolerate a wide range of water conditions in modified habitats (Loman and Lardner 2006), specific phases of development may be bottlenecks in modified habitats (see Section 3.4).

One correlate of forest fragmentation that may have profound effects on anuran communities is decreased opportunity for reproduction (Zimmerman and Bierregaard 1986). Forest anurans have complex and diverse modes of reproduction (Donnelly and Guyer 1994), but many species can be coarsely classified as pond-breeders and litter dwellers, the latter referring to those species with modes of reproduction that do not depend on sources of standing water (Donnelly 1998). Small forest fragments may not contain bodies of water proper for reproduction, and thus force individuals, perhaps even on a daily basis, to travel back and forth to breeding grounds. Doing so generates a physiological challenge whose magnitude relates to the conditions of the open areas surrounding fragments, particularly water availability and temperature, and to the distance between forest fragments and water bodies. How challenging a specific site is, then, depends on landscape ecology, mainly distance among patches (Brown and Kodric-Brown 1977), characteristics of the environment surrounding them (Fahrig and Merriam 1994, Gascon *et al.* 1999), and the number of corridors connecting patches (Lima and Gascon 1999).

It is generally believed that the threat of habitat fragmentation for anuran amphibians is worsened because of site fidelity and limited ability for dispersal (Blaustein *et al.* 1994, Marsh and Pearman 1997, Smith and Green 2005). The community of pond-breeding anurans in small fragments is likely to be composed mainly by the species with better ability to reach breeding grounds and circulate among neighboring fragments (Becker *et al.* 2007), which is a partial function of body size and metabolic physiology. The body of literature dedicated to the physiology of anuran locomotion shows dramatic differences among species in power and stamina that relate to the biochemical profile of leg muscle fibers (Taigen *et al.* 1982, Taigen and Pough 1985, Pough and Taigen 1990). Because these and other traits of exercise physiology determine the ability for locomotion of anurans, they should influence also the genetic flow among anuran populations isolated in forest fragments, independently of their mode of reproduction. Despite the importance of understanding whether exercise physiology influences amphibian vulnerability to habitat fragmentation, we were unable to detect studies carried with this purpose.

3.6. Exotic species

Human activity has been historically associated with the deliberate or accidental transport of animal and plant species outside their natural ranges, and to related changes in local patterns of biodiversity (Lonsdale 1999, Mack *et al.* 2000, McKinney 2002a, b). Exotic species may affect local diversity through their interactions with native species, particularly when their introduction occurs concomitantly with human-related ecological deterioration (Sax and Gaines 2003, Williamson 1996, Lonsdale 1999). Tolerance to anthropic environments is a characteristic of two anuran species that are currently considered feral pests in several parts of the world, the cane toad (*Chaunus marinus*) and the Bullfrog (*Lithobates catesbeianus*). The bullfrog is the principal invasive alien species in Brazilian amphibian communities (Guix 1999, Fortes *et al.* 2004, Rocha-Miranda *et al.* 2006), a process that has been facilitated by artificial dispersal related to teaching and aquiculture (Guiz 1999, Rocha-Miranda *et al.* 2006). The first Brazilian bullfrog cultures were established in 1935 (ISSG, 2005), and feral populations in State of São Paulo were detected in 1988 (Bruneau and Magnin 1980, Bury and Whelan 1984). Although froglets feed mainly on insects (Minton 1949 *apud* Guix, 1999), adults are voracious predators of crustaceans and other small or young vertebrates, including other anurans (Guix 1999). Bullfrog tadpoles may feed on eggs and larvae of other anuran species (Ehrlich 1979), but tend not to be palatable to many local predators (Rocha-Miranda *et al.* 2006). Bullfrogs may also offer indirect risk to local anurans, as the colonization of natural areas by this species may contribute to the dispersal of disease, including chytridiomycosis (Mazzoni *et al.* 2003, Hanselmann *et al.* 2004). All these traits enhance the possible role of this invasive species as a threat to the local anuran fauna (Jim 1997, Guix 1999, Rocha-Miranda *et al.* 2006).

The success of feral species to colonize given environments appears to follow some broad ecological rules, but at the same time is case-specific. On one hand, invasion biologists have proved that the species richness of a community relates to the likelihood of invasion by exotic species (Stohlgren *et al.* 1999, Meiners *et al.* 2004, Chown *et al.*, 2005). Studies in the Southern Ocean Islands showed that energy flow into the islands relates positively to the diversity of both indigenous and exotic species. This appears to be so because favorable local energetic conditions, which are in turn associated with greater niche partitioning, favor diversity independently of whether the components of modified communities are native or exotic (Chown *et al.*

2005). On the other hand, some exotic species are far more likely than others to dominate new settings to the point of changing ecosystem structure and functioning (D'Antonio and Dudley 1995, Mack *et al.* 2000).

Why some exotic species have the physiological and behavioral ability to outcompete local species is a question that lies in the interface between physiology and invasion biology. From one point of view, some successful invasive species may have traits of physiology that make them particularly competitive in new environments. These may relate to reproductive output and growth rates, but also to subtle aspects of physiology. For example, tadpoles of *L. catesbeianus* can recognize and react to cues of novel predators, and this neural ability may favor its capacity to colonize novel settings (Pearl *et al.* 2003). It is also possible that the ability of species to gather and process energy affects the results of ecological interactions. One case study that has received particular attention is the interaction between introduced bullfrogs on populations of the native California red-legged frog *Rana aurora*. Although bullfrogs usually cause declines of *Rana aurora,* the negative effects of this introduced species are more dramatic when food resources are clumped and almost negligible when resources are scattered through the ponds. One conclusion is that the mechanisms by which exotic anuran species affect native frogs need not to be direct or obvious (Adams 2000); furthermore, such effects may include reaction norms of physiological processes. Tadpoles of native species may respond with different shifts in level of activity and growth rates to the presence of *L. catesbeianus* tadpoles and these differences may affect the competitive interactions with native and introduced species (Monello *et al.* 2006).

4. The Brazilian Scenario

The global phenomenon of decline and extinction of amphibian populations has not spared Brazil (Heyer *et al.* 1988, 1990, Weygoldt 1989, Haddad and Sazima 1992, Bertoluci and Heyer 1995, Young *et al.* 2001, Eterovick *et al.* 2005), and is evident even in protected areas regularly visited since the 1970s (Heyer *et al.* 1988, Weygoldt 1989, Bertoluci and Heyer 1995, Pombal and Haddad 1999, Eterovick *et al.* 2005). The reasons for the decline of Brazilian anurans are largely unknown, but possible causative agents include habitat fragmentation, pollutants, infections, climatic changes, invasion by feral species, wildlife trade (Silvano and Segalla 2005), and possible synergistic effects among some or all these factors (Young *et al.* 2001). The climatic conditions of Brazil offer large extensions suitable for the action of the pathogen fungus *B. dendrobatidis* (Carnaval *et al.* 2006, Toledo *et al.* 2006a, b) and 23 species have been reported as infected by this fungus in the Brazilian Atlantic forest (Carnaval *et al.* 2006, Toledo *et al.* 2006a, b). Scientists speculate about a possible expansion to the Cerrado and the Pantanal (Ron 2005, Toledo *et al.* 2006a, b), but little is known about the current distribution of *B. dendrobatidis* in Brazil and its possible consequences to local species (Toledo *et al.* 2006a, b). Discussing cause-effect relationships associated with declines of Brazilian anurans is difficult because of inadequate information about natural history and ecology, particularly in terms of long-term monitoring (Silvano and Segalla 2005). This situation is further complicated by the size of the country, the diversity of its anuran fauna (Silvano and Segalla 2005), and the meager information available on the physiological ecology of Brazilian anurans. It is symptomatic of these problems that we were unable to find records about effects of common toxic compounds, such as pesticides, on Brazilian amphibian species. The absence of data, in this case, supports the claim by Schiesari *et al.* (2007), that areas with high amphibian diversity have received very little attention regarding the consequences of pollutant spill (see Section 3.5).

The problem of habitat fragmentation is well illustrated in Brazil by the natural history of Atlantic forest, although other biomes such as the Cerrado also deserve attention (Brasileiro *et al.* 2005). The Atlantic forest is the richest Brazilian biome in terms of anuran fauna, and shelters more than 300 species, many of which are endemic (Duellman 1999). During the past three decades, this biome has been fragmented and altered (Pinto and Brito 2005) to a point where only about 5% of the original area remains as fragments of diverse sizes (SOS Mata Atlântica, 1998). The fragmentation of the Atlantic forest may be less stressing for species that do not require ponds for reproduction, such as members of the genus *Eleutherodactylus* (Brachycephalidae), but is likely to affect species requiring ponds or streams (Heyer *et al.* 1990, Becker *et al.* 2007). When bodies of water are excluded from Atlantic forest fragments, anurans that persist because of either their ability to tolerate the ecological conditions of gaps, or their capacity for locomotion, may have an advantage (see Section 3.5). Although we defend emphatically the importance of studies aiming to identify the ecological outcome of fragmentation for anurans of the Atlantic forest, a necessary extension in scope requires understanding why some forest species tolerate the physical changes associated with fragmentation better than others. For example, comparative studies of the physiology of species adapted to natural forest gaps and inside forest may help in understanding which species, and why species are affected by deforestation (Haddad *et al.* 2007). Overall, animal physiological adaptation to the Atlantic forest has been largely overlooked despite its importance for conservation (Navas *et al.* 2007b).

The effects of climate change in Brazil have been discussed mainly in terms of transformation of lands for agriculture (Cerri *et al.* 2007), but recent efforts have been devoted to understanding comprehensive effects on biological diversity (Marengo 2006). As discussed in Section 3.2, global warming and extreme climatic events run in parallel, so it is worth asking to which extent atypical climatic events may have already influenced the anuran fauna of Brazil. According to Heyer *et al.* (1988), a severe frost may have had a dramatic effect on the anuran communities of Southeastern Brazilian Atlantic forest. From data spanning 35 years, Heyer and collaborators observed drastic declines in the populations of *Hyalinobatrachium eurygnathum, Scinax perpusillus, Leptodactylus marmoratus, Eleutherodactylus guentheri, E. parvus,* and *Hylodes phyllodes* populations, and also registered the extinction of *Crossodactylus dispar, Cycloramphus boraceiensis, C. semipalmatus, Hylodes asperus* and *Thoropa taophora*. The reported population crashes coincided with a four-day long frost that occurred in 1979 during which temperatures dropped to -2.6°C. Whereas some species that were decimated in 1979 (Heyer *et al.* 1988) recovered as to be considered abundant again (*S. perpusilla* and *Hylodes phyllodes*; Bertoluci and Heyer 1995), others disappeared (*C. dispar, C. gaudichaudii, C. boraciencis, C. semipalmatus, H. asperus* and *T. taophora*; Bertoluci and Heyer 1995). Other cases of population declines in Brazilian frogs have been attributed to unusually dry winters (Weygoldt 1989); it seems clear that short-term but extreme climatic events may become part of the evolutionary history of anurans and affect their distribution (Vanzolini and Williams 1970, Heyer *et al.* 1988). Still, we must ask why some species, among the many equally exposed to such extremes through time, are particularly sensitive to cold. Hot temperatures may also affect Brazilian anurans, particularly those in semi-arid habitats (see Section 3.2). Postmetamorphic toads from the Brazilian Caatinga, a hot semi-arid biome in Northeastern Brazil, are diurnal and disperse by hopping over long distances on hot substrates. These toads exhibit the highest thermal tolerance reported for anurans, yet are active at conditions close to their thermal tolerances (Navas *et al.* 2007a). They are unlikely to tolerate the 2-5ºC increase in mean temperature, and the concomitant decrease in humidity, predicted for the Caatinga at the end of the 21st century (Marengo 2006).

It is worth noting that some anuran species, native or invasive, benefit from environmental changes resulting from human activities. For example, anurans that lay eggs in still water, or that lay eggs protected by foam nests, may be more tolerant to regional temperature shifts (Haddad and Prado 2005, Haddad *et al.* 2007). As far as such bodies of water are seasonally available, these species may occupy areas otherwise becoming more arid (see Haddad *et al.*, 2007). Bullfrogs are very competitive in warm and open ponds and by the side of rivers in modified environments, which are common in Brazil. Asking why bullfrogs are favored in areas exposed to human impact; whether they are, as it seems, less susceptible to pollutants than most native species, or whether their tadpoles are physiologically more capable than those of native species, may bring new insights to explain the success of this exotic species. Reproductive output is an issue too because in comparison with individuals within the natural range, Brazilian bullfrogs exhibit longer reproductive periods and higher growth rates (Fortes *et al.* 2004). These shifts in natural history may be just the passive consequence of exposure to warmer conditions and the absence of a winter, but they may reflect as well adjustments in the thermal biology of the species to tropical conditions. Brazilian bullfrogs, and alien species in general, constitute a valuable resource to understanding why some species are more successful at invading new areas than others, and how the patterns of relative success might change as both local and regional environments change (Frenot *et al.* 2005).

The conservation of Brazilian anurans would benefit from studies using a number of techniques that, although quite restricted in the country, have proven useful to monitor or predict physiological shifts along ecological gradients. These include 1) the combination of physiological research with biophysical modeling to identify how large-scale climatic variables may affect individual organisms (Spotila *et al.* 1992, Bartelt and Peterson 2005, Helmuth *et al.* 2005), 2) data logging to monitor physiological responses to environmental variables (Block 2005), and 3) integration of studies in physiological ecology with data coming from Geographic Information Systems (GIS). Spatial data from GIS allow graphical display and analysis at a large scale, and have proven valuable to understand how human activity affects animal energetics and ecological success in disturbed environments (Porter *et al.* 2000). As examples, combined data from GIS and experimental physiology have been used to predict the areas in which the conditions of humidity and temperature are appropriate for successful hatching in a lizard species (Porter *et al.* 2000), and the potential distribution of introduced species such as *Chaunus marinus* in Australia (Sutherst *et al.* 1996).

5. Conclusions

As previous authors have pointed out (Blaustein *et al.* 2002), it is often difficult to assign a single cause to the decline of an anuran population because some noxious factors act in the long term, and because synergistic interaction among environmental variables obscure individual effects. Independent of these problems, the examples of environmental change highlighted in this review would benefit by further studies in thermal biology, water balance, exercise physiology, thermal physiology, endocrinology, immunology, and metabolic physiology. Studies in physiological ecology are of remarkable practical value to understand the susceptibility of anurans to environmental extremes, including retrospective studies where preserved specimens and climate records are available. Comparative physiology would help to explain the underlying mechanisms supporting these differences among species, and evolutionary physiology could elucidate the scope and constraints of possible adaptive change. All these topics and approaches converge at conservation physiology, and may generate important applicable information to understand anuran declines and improve management decisions.

One conclusion emerging from our analysis is the need for integration, and the potential value of studies involving cooperation between ecologists and physiologists. Despite the huge body of literature on anuran thermal biology, for example, it is still difficult to assess how changes in climate may affect the overall reproductive output, particularly in species that hibernate or aestivate. Physiological ecology associated with habitat fragmentation is also a very constructive field of research. By investigating the environmental conditions of the gaps and the physiological tolerance of anuran species to these conditions we could answer questions such as how far or for how long can individual anurans successfully progress into the gaps between habitat fragments? To what extent do basic corridors that improve shade and humidity help to connect isolated forest populations? Although it is clear that habitat loss and fragmentation affect amphibian performance, survival, and reproductive success, we need to understand why in order to improve management. Interdisciplinary studies may also help to elucidate complex patterns, for example possible interaction between fragment area, arthropod diversity, diet, skin peptides, and microbial defense in anurans.

Brazil is already well-prepared with infrastructure, databases, and ecological background to make anuran conservation physiology a particularly successful enterprise. An additional advantage is the diverse geography and large extension of the country, given that species distributed along significant ecological gradients are of special value to predict the types of changes that would occur because of environmental change such as global warming (Miles 1994, Donnelly 1998). Brazil also has the potential to support studies aiming to elucidate which combinations of ecophysiological factors (e.g., activity temperature, dependence on soil moisture, and skin permeability) affect the likelihood of a chytridiomycotic infection, what are the consequences of global climate change to anurans, and why various specific fractions of the original community survive in forest fragments of different sizes. These and many other questions in conservation physiology can readily be converted into testable hypotheses that would greatly contribute to conservation and management of Brazilian anurans.

Acknowledgements

We are grateful to Célio Haddad and Catherine Bevier for constructive criticisms and comments on a first version of this manuscript. During the writing of this paper C. A. Navas was supported by the State of São Paulo Science Foundation (FAPESP), grant 2003/01577-8.

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