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The ongoing invasion of African clawed frogs (*Xenopus laevis*) in Chile: causes of concern

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Abstract. We review the existing data on the African clawed frog in Chile (*Xenopus laevis*, Pipidae) and report new and alarming information on its distribution, provide physical data on water courses and bodies that hold populations of this frog, report observations on its diet, on mass migration overland, and on predation by native birds. Our findings reveal that: (a) the spread of the invasion is currently covering 4 of the 13 regions of Chile; (b) clawed frogs are found at higher densities in artificial water bodies (ponds and dams and irrigation canals) rather than in natural lagoons or streams or rivers; (c) there is no evidence of predation on native anurans, but rather on their own larvae; (d) they face predation from native birds. Causes of concern include (a) that African clawed frogs in Chile reach both lower and higher altitudes than formerly estimated, and (b) that they are able to migrate overland to colonize other water bodies. They are spreading at a rate of 3.1–3.9 km/year in an optimistic scenario, and at a rate of 4.4–5.4 km/year in a pessimistic one. The most troubling aspects of the African clawed frog invasion in Chile involve: (a) their unaided spread through central Chilean agricultural areas, using irrigation canals and overland migration; and (b) the type of interactions that they may be establishing with native anurans (are they competitors, predators, habitat modifiers, disease vectors, or all things together?). As a precautionary action, we propose that the pet trade of African clawed frogs in Chile should be banned.

Introduction

The African clawed frog (*Xenopus laevis*) was introduced to Chile in 1973, when an unknown number of frogs were dumped into Caren lagoon, close to Santiago's international airport (Jaksic 1998). This is the only known introduction, although translocations to other water bodies seem to have been effected from Caren lagoon afterwards. Since 1973, in addition to translocations, the clawed frog spread on its own to other lagoons, ponds, dams and watercourses around Santiago (Metropolitan Region), and also west to the V Administrative Region of the country and south to the VI Region (Lobos 2002). Fear has been expressed about the effects of this invasive alien species on the native aquatic fauna (Glade 1983), because central Chile is a recognized biodiversity hotspot (Myers et al. 2000) and particularly because the country harbors only 43 species of amphibians (all of them anurans), of which 33 (77%) are endemic to Chile (Formas 1995). In spite of this preoccupation, Jaksic (1998) noted that ''No information exists on the possible effects of the introduction of the African clawed frog on sympatric native fauna in central Chile''.

But information has slowly been accumulating since 1998. Lobos et al. (1999) documented the first dietary data, Lobos (2002) reported specific localities where the clawed frog was found, and Lobos and Garin (2002) communicated the first record of one such frog dispersing overland. Recently, Lobos and Measey (2002) collected first-hand information on distribution, density and diet in central Chile. They reported that the clawed frog is recorded in four administrative regions of the country (Metropolitan, V, VI and VIII Administrative Regions), that its density ranges between 0.25–0.37 frogs per square meter in suitable ponds of the Metropolitan Region, and that its diet in the same Region comprises chiefly zoobenthic and zooplanktonic taxa, mostly Chironomids, Ostracods and *Physa* snails.

In this paper, (a) we review the existing data on the African clawed frog in Chile, (b) report new and alarming information on its distribution; (c) provide physical data on water courses and bodies that hold populations of this frog; and report observations on (d) its diet; (e) mass migration overland; and (f) predation by native birds.

Methods

Part of our work is a review of previous studies, another is presentation of new data. Specific methods for the review part may be traced to the original reports. What follows is a brief summary of methods by topic.

Distribution and habitat. We surveyed localities in central Chile, specifically in the Metropolitan Region (11 sites), and in the contiguous IV (9 sites), V (5 sites) and VI Regions (1 site). Geographical parameters (latitude, longitude, elevation) of the 26 localities scrutinized are given in Table 1. Physical–chemical parameters of water (water temperature, dissolved oxygen, pH, and electric conductivity) were obtained in 8 of the 26 sites (see Lobos (2002) for details).

Diet. A sample of 111 stomachs from four localities was examined: Laguna de Batuco, Cuesta de Ibacache, Antumapu and Vertiente Cerros de Batuco, all in the Metropolitan Region (see Table 1 and Lobos et al. (1999) for details).

Migration and predation. Overland movements of clawed frogs were measured at Rinconada de Maipu, in the Metropolitan Region (see Table 1) on 2 and 3 December 2002. Predation records totaling 12 h of observation were obtained at the same site from a blind from 5 to 20 November 2002, using 10×42 binoculars during daytime and a no-magnification night-viewing device during nighttime. Feces and regurgitated pellets of potential predators of clawed frogs were collected opportunistically.

Results

Distribution

We found that Lobos and Measey (2002) were misled by Hermosilla (1994) in reporting the presence in the wild of African clawed frogs in Chile's VIII

Table 1. Geographic, physiognomic and physical–chemical characteristics of 26 sites with or without African clawed frogs in central Chile (ordered in north–south sequence).[a]

Site	Latitude/longitude	Elevation	Physiognomy	Water temperature	Dissolved O_2	pH	Conductivity	*Xenopus*
IV Region								
Sector las Compañias	29°53′S 71°14′W	50	Lothic, stream	nd	nd	nd	nd	No
Ovalle	30°36′S 71°12′W	200	Lentic, artificial pond	nd	nd	nd	nd	No
Barraza	30°39′S 71°29′W	55	Lothic, stream	nd	nd	nd	nd	Yes
Camaronera	30°40′S 71°31′W	50	Lentic, artificial pond	nd	nd	nd	nd	Yes
El Salitre	30°40′S 71°31′W	50	Lentic, artificial pond	nd	nd	nd	nd	Yes
Salala	30°42′S 71°35′W	50	Lothic, stream	nd	nd	nd	nd	Yes
Chalinga	30°44′S 71°25′W	125	Lothic, stream	nd	nd	nd	nd	No
Huentelauquen	31°35′S 71°32′W	35	Lothic, stream	nd	nd	nd	nd	No
Estero Chigualaco	31°45′S 71°30′W	60	Lothic, stream	nd	nd	nd	nd	No
Metropolitan Region								
Laguna de Batuco	33°12′S 70°50′W	485	Lentic, lagoon	22.0	3.7	7.4	1980	Yes
Vertiente Cerros de Batuco	33°12′S 70°50′W	500	Lothic, cold spring	21.3	4.6	7.3	760	Yes
Laguna Quinta Normal	33°26′S 70°42′W	520	Lentic, artificial pond	nd	nd	nd	nd	Yes
Laguna Caren	33°26′S 70°50′W	450	Lentic, lagoon	nd	nd	nd	nd	Yes
Cuesta de Ibacache	33°27′S 71°20′W	300	Lothic, cold spring	19.6	7.4	7.8	398	Yes
Rinconada de Maipu	33°29′S 70°54′W	470	Lentic, irrigation dam	11.0	3.6	8.8	129	Yes
Sector Lonquen	33°34′S 70°49′W	420	Lentic, irrigation dam	nd	nd	nd	nd	Yes
Cerros de Chena	33°35′S 70°44′W	510	Lentic, irrigation dam	nd	nd	nd	nd	Yes
Antumapu	33°37′S 70°39′W	620	Lentic, irrigation dam	27.0	3.1	8.6	617	Yes
Huelquen	33°50′S 70°38′W	401	Lentic, irrigation dam	26.5	2.6	7.9	82	Yes
Laguna de Aculeo	33°50′S 70°55′W	350	Lentic, lagoon	nd	nd	nd	nd	Yes
V Region								
Estero de Cordoba	33°26′S 71°39′W	30	Lothic, stream	nd	nd	nd	nd	Yes
Rio Maipo	33°36′S 71°37′W	10	Lothic, river mouth	nd	nd	nd	nd	Yes
Ojos de mar at Llolleo	33°36′S 71°37′W	10	Lentic, salt lagoon	23.6	3.1	9.4	1856	Yes
Tranque Leyda	33°37′S 71°29′W	200	Lentic, irrigation dam	nd	nd	nd	nd	Yes
Tranque de San Juan	33°38′S 71°32′W	50	Lentic, irrigation dam	25.3	2.3	7.9	147	Yes

Table 1. (continued)

Site	Latitude/longitude	Elevation	Physiognomy	Water temperature	Dissolved O_2	pH	Conductivity	*Xenopus*
VI Region								
Lago Rapel	34°05′S 71°32′W	70	Lentic, large dam	nd	nd	nd	nd	Yes
Range	29°53′S-34°05′S	10–620	Not applicable	11.0–27.0	2.3–7.4	7.3–9.4	82–1980	

[a]Units are: elevation (m), temperature (°C), dissolved oxygen (ppm) and electric conductivity (mg/l).

Administrative Region. Dr. Juan Carlos Ortiz (in litt.) informed us that the clawed frog is found only in laboratories of the University of Concepcion. But we found clawed frogs in four of nine localities surveyed in the IV Administrative Region. Interestingly, those frogs were captured only in the Limari river basin, and not in the Choapa river basin to the south or the Elqui river basin to the north. Therefore, clawed frogs were not advancing from the south on their own, but were likely translocated to the Limari River, for reasons unknown. The absence of these frogs from the Elqui River sets their northernmost limit around Barraza (30°39′S) near the city of Ovalle. Thus, the extent of the invasion of clawed frogs in Chile is still constrained to four contiguous regions in the central part of the country (IV, V, VI and Metropolitan), although there is risk associated with the presence since the 1980s of laboratory frogs in a major university of the VIII Region.

Habitat

We surveyed the presence of African clawed frogs in central Chile (Table 1) and found that they are present more often in lentic (15 of 16 = 94% of sites) than in lothic waters (6 of 10 = 60% of sites). Out of 15 lentic sites with clawed frogs, they are present mostly in irrigation or multipurpose dams and in artificial ponds (80% of occurrences) versus 20% in natural lagoons. Veloso and Navarro (1988) stated that this frog is found at elevations ranging between 250–500 m, but our results show that it reaches from almost sea level up to 620 m (Table 1). In addition, clawed frogs inhabit quite a diverse array of habitats with regard to water temperature, dissolved oxygen, pH, and electric conductivity (Table 1), indicating a high degree of adaptability and colonization potential.

Diet

The first information on the diet of African clawed frogs in Chile was reported by Lobos et al. (1999) in a rather obscure Chilean journal. They documented highly detailed profiles of the diet in four local populations in central Chile, based on a sample of 111 stomachs. Here we present a less detailed overview, which nonetheless gives an idea of the major food items found in local populations, and of their geographic variation. In central Chile, clawed frogs prey on essentially three major food types: insects, mollusks and crustaceans (Table 2). Similar findings have been reported in the US (McCoid and Fritts 1989) and the UK (Measey 1998a). A substantial fraction of insects in the Chilean diet is made up of Chironomids, mostly as larvae but also as pupae (Table 2). Mollusk prey is dominated by a single species, *Physa* sp. Crustaceans are mainly Ostracods. The only vertebrates found in local diets are *Xenopus* larvae (Table 2). A perspective on where in their habitat clawed frogs capture prey is gained by analyzing their diet by prey type rather than by taxon (Lobos and Measey 2002). Clawed frogs at our study sites preyed chiefly on benthic prey (Table 3), which are essentially sedentary, suggesting that these frogs

Table 2. Summary of prey by taxon in the summer diet (November 1997 to February 1998) of African clawed frogs at four sites of central Chile (the first three are natural, the fourth is artificial).[a]

Prey taxa	Sites			
	Laguna de Batuco	Vertiente Cerros de Batuco	Cuesta de Ibacache	Antumapu
Insects	56.1	24.0	84.1	17.6
Mollusks	37.5	5.8	1.3	64.2
Crustaceans	3.5	70.2	11.6	18.0
Vertebrates (all *Xenopus*)	2.9	0.0	1.0	0.0
Annelids	0.0	0.0	1.5	0.0
Arachnids	0.0	0.0	0.5	0.2
Total prey	856	121	1032	642
No. of stomachs	51	5	32	23
Stomachs with plant parts (%)	33.0	0.0	56.2	39.1
Stomachs with microalgae (%)	100.0	100.0	100.0	100.0
Stomachs with *Xenopus* (%)	21.6	0.0	25.0	0.0

[a]Percentages are by number of prey items, not by biomass. Geographic location of sites as in Table 1.

Table 3. Summary of prey by type in the summer diet (November 1997 to February 1998) of African clawed frogs at four sites of central Chile (the first three are natural, the fourth is artificial).[a]

Prey types	Sites			
	Laguna de Batuco	Vertiente Cerros de Batuco	Cuesta de Ibacache	Antumapu
Zoobenthos	62.6	80.0	74.61	57.8
Zooplankton	3.2	10.2	17.9	24.0
Nekton	27.2	5.2	5.4	14.9
Terrestrial	4.1	3.5	2.0	3.3
Xenopus	2.9	1.1	0.0	0.0

[a]Percentages are by number of prey items, not by biomass. Geographic location of sites as in Table 1. Total prey and number of stomachs the same as in Table 2.

forage at the bottom of ponds. Nevertheless, mobile prey in the nekton was a secondary diet category (Table 3), suggesting that clawed frogs also actively forage in the water column. Terrestrial prey found in the diet (Table 3) may have just fallen to the water, or may have been captured on land (Measey 1998b).

Migration

The African clawed frog is considered to be completely aquatic at all stages of its life history, but several reports of overland migration during torrential rain have been documented (Tinsley et al. 1996). This may explain how clawed frogs have colonized isolated ponds in California, USA (McCoid and Fritts 1980a,b) and why previously marked individuals have been retrieved away from first-capture ponds in the UK during summer (Measey and Tinsley 1998). Lobos and Garin (2002) were the first in Chile to report that a juvenile clawed frog was captured at a rodent trap placed in a dry irrigation canal, 1500 m away from the nearest pond, and 170 m from the nearest ditch with standing water. The trap was activated at dusk and the frog was captured at dawn, thus revealing that it migrated during the night. It was spring and had not rained in the preceding days.

We took advantage of the presence of a drying dam at Rinconada de Maipu during summer 2002, to observe what happened with clawed frogs therein. This dam was previously studied by Lobos and Measey (2002). By April 2001 water covered 79,000 m^2 and its depth was about 3 m. The dam had to be drained to counter the torrential downpours of winter 2002 so that by November 2002 its water-covered surface was only 7500 m^2, and only 1 m deep. By 2 December 2002 the once continuous water body had become a collection of small isolated pools 5–15 cm deep. At 10:00 an intense exchange of frogs among pools was observed. From 12:00 to 17:00 a few frogs were observed moving southwards toward a canal about 100 m to the south. Most of the frogs were either dehydrated or dying. At 22:00 a massive displacement of frogs occurred southwards. Three columns moved straight toward the canal, negotiating the dam's retaining wall (which raised 8 m at 45° angle, was topped by a 2 m level expanse and then tapered by 31 m at a 60° angle). Sixty-four meters of abandoned, flat agricultural field separated the dam from the irrigation canal. A fourth column of frogs took an eastward route of 96 m that avoided the retaining wall and then moved southward for an extra 80 m across an abandoned field. A sample of migrating frogs revealed that they were in good body condition, and that they were subadults and adults of both sexes (no juveniles were observed migrating, although they were present in the pools). From 23:00 to 24:30, four transects of 50 m × 4 m were visually surveyed parallel to the dam and to the canal. The two transects by the dam (frog source) yielded 290 and 320 individuals, whereas those by the canal (frog sink) yielded 52 and 64 individuals. By morning of 3 December 2002 few frogs were still at the pools behind the dam, and a handful of dead frogs were found lying on the open field between the dam and the canal. Most frogs apparently succeeded in reaching the irrigation canal and scattered up and downstream.

Predation

It has been hypothesized that the African clawed frog is little preyed upon because of its toxic skin (McCoid and Fritts 1980a). We examined the incidence of predation in a drying dam in Rinconada de Maipu (referred to above). Three bird species were observed to prey on clawed frogs: Night heron (*Nycticorax nycticorax*), Kelp gull (*Larus dominicanus*) and Burrowing owl (*Speotyto cunicularia*). Night herons congregated around the dam starting at 18:00 every evening, reaching up to 44 individuals. We observed 18 capture attempts of clawed frogs by herons by (a) standing and waiting in the periphery of the dam (4 successes, 3 failures); (b) walking slowly in the dam (5 successes, no failures); (c) swimming in the dam (1 success, 1 failure); (d) flying over the dam (3 successes, 1 failure). Herons ate the belly (especially female gonads) and loins of frogs, not consuming the skeleton or legs. Kelp gulls numbered one to three pairs at the dam. We observed 12 capture attempts of clawed frogs by (a) swimming in the dam (7 successes, 2 failures) and (b) flying over the dam (3 successes, no failure). Unlike herons, gulls could not kill frogs with a single strike of their bill. They had to give several strikes to the skull, taking up to 10 min to kill a frog. We detected only one pellet of Burrowing owl that contained clawed frog remains. One Great egret (*Casmerodius albus*), reputedly a frog eater, was observed at the dam, but was not detected attempting to capture clawed frogs. Other species that were found at the dam but that were not detected attacking clawed frogs were the ducks *Anas sibilatrix*, *Anas bahamensis* and *Anas georgica*, the gull *Larus maculipennis* and the Black-necked stilt *Himantopus mexicanus*. There were no fishes at the dam, neither native nor introduced.

Discussion

The African clawed frog has been an impressive invader in California, USA, on account of its rapid colonization of suitable sites (McCoid and Fritts 1980a), explosive reproduction (McCoid and Fritts 1980b), and consumption of native prey (McCoid and Fritts 1989; Lafferty and Page 1997; Crayon, in press). A similarly rapid invasion has been taking place in Wales, UK, as documented by Measey (1998a, 2001) and Measey and Tinsley (1998). With regard to the ongoing invasion of African clawed frogs in Chile, the news is mixed. Some relief may be found in that (a) the spread of the invasion does not include the southern VIII Region of the country; (b) the clawed frogs seemingly prefer artificial water bodies (ponds and dams and irrigation canals) rather than natural lagoons or streams or rivers; (c) they apparently are not eating native frogs, but rather their own larvae; and (d) they face predation from native birds. But causes of concern lie in that African clawed frogs in Chile are now present in the IV Region, they reach both lower and higher altitudes than formerly estimated, and they are capable of moving overland to colonize other water bodies.

Distribution and migration

The risk posed by advancing clawed frogs all over the Metropolitan and adjoining IV, V and VI Regions cannot be downplayed. In the past, there was suspicion that wildlife dealers in central Chile were stocking these frogs in ponds, dams and lagoons for sale to pregnancy clinics and biomedical laboratories, as test animals (Galli Manini's Test). But clawed frogs are not used in Chile for these purposes since the advent of pregnancy kits early in the 1980s. More and more frequently, they have been showing up in the local pet trade, and their private owners are suspected of dumping them in the nearest water course or body once the frogs become too large to hold in small aquaria. Therefore, there is a continuous restocking of clawed frogs around the most populated areas in Chile (Santiago and Valparaiso; but apparently not so in Concepcion as of yet). One way to reduce this risk would be to ban the sale of clawed frogs in pet shops.

Another problem is that once introduced or translocated, African clawed frogs move around unaided by humans. They seem to be taking advantage of the extensive irrigation system in place in central Chile. Indeed, our finding that these frogs may move massively overland is particularly troubling, because it means that their invasive potential is even greater than suspected. The common practice of emptying dams once a year (to extract silt) may aggravate the situation by forcing clawed frogs to migrate off periodically.

Because the release point of clawed frogs is well known and dated (Caren Lagoon, September 1973), it is possible to calculate their rate of spread. To the west it has proceeded 75 km, at about 3.1 km per year, conservatively considering that frogs reached the farthest point in about December 1997 (=24 yr). By the same token, they have expanded 97 km to the south at 3.9 km/yr (farthest point conservatively estimated as reached in about November 1998 = 25 yr). Nevertheless, according to Veloso and Navarro (1988), African clawed frogs did not become naturalized until 1980, which would set the starting point of the invading wave 7 years later than mentioned above. If this were the case, frogs would be expanding westwards at 4.4 km/yr and southwards at 5.4 km/yr, that is, at rates 38–42% higher. The possibility that there have been additional translocations by humans is a common occurrence with many introduced species. Therefore, all calculations of spread rate should be taken with caution.

To the north of the V Region there is little potential for natural expansion of African clawed frogs, because of the semidesertic character of that part of Chile, which in addition is little irrigated except around the three major rivers that traverse the IV Region. Nevertheless, purposeful translocation by humans looms as a menace for aquatic systems of the IV Region. To the east, clawed frogs have already reached the Pacific coastline, and to the west they face the insurmountable Andean Ranges. Thus, all new natural expansion should be toward the south of Region VI. This is troublesome, because Regions VII and VIII as well as the northern part of Region IX are covered by innumerable irrigation systems, the climate is temperate, and the diversity of native frogs peaks around Regions VIII to X. The ca. 450 km separating Rancagua (VI Region) from Concepcion (VIII Region) could be covered by African clawed frogs in less than a century; much less if aided by humans.

Habitat, diet and predation

Our diet results point to cannibalism by African clawed frog, and to apparent lack of predation on larvae or adults of sympatric native frogs. The frequent presence of parts of aquatic plants and of microalgae in the stomachs analyzed suggests that they are ingested together with other more substantial prey. In general, the diet reported here for four populations coincides taxonomically to a large extent with that documented by Lobos and Measey (2002) for a population at Rinconada de Maipu, based on a sample of 21 stomachs collected in March 2001. At this latter site, though, Crustaceans dominated at 95.2% of the diet by number, with Chironomids accounting for 3.0%, *Physa* snails for 0.1%, and other taxa combined for 1.7%; no vertebrates were part of the diet in this case (Lobos and Measey 2002). Therefore, there is plenty of variation in the diet of clawed frogs in central Chile, at least with regard to prey relative frequency if not to prey taxonomic composition.

Clawed frogs do not seem too prone to invade natural watercourses or water bodies, but they occasionally do. Therefore, they must get in contact with native fauna, including other amphibians as well as fishes, most of them considered endangered (Glade 1983). The competitive potential between alien and native frogs cannot be currently appraised, but the predation potential of clawed frogs is troublesome. Although the samples analyzed to date fail to demonstrate consumption of vertebrates other than their own larvae, it must be recognized that the potential exists. The most alarming scenario would be that native amphibians fail to appear in clawed frog diet simply because they have already disappeared from aquatic environments invaded by the alien frog.

The finding that native predators consume African clawed frogs is hopeful. But it should be taken into consideration that all our data come from a drying dam, which may have attracted predators because of the increasing concentration of clawed frogs brought about by decreasing depth. In addition, native predators may not be able to control the invasive frog, simply because it is already too numerous and reproduces too quickly.

Future directions

There are two troublesome aspects of the African clawed frog invasion in Chile. The first one involves its unaided spread through central Chilean agricultural areas, using irrigation canals and also migration overland. A more thorough survey of both artificial and natural water bodies is called for in order to determine the real spread of the invasive fronts. Secondly, the type of interaction that may be occurring between alien and native anurans needs to be determined. Are African clawed frogs competitors, predators, habitat modifiers, disease vectors, or all things together? Water bodies shared by clawed frogs and native amphibians should be located and studied in order to gauge the impact that the former may be having on the latter. Until these aspects are resolved, the pet trade of African clawed frogs in Chile should be banned.

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