ELSEVIER

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Demography of *Quasipaa* frogs in China reveals high vulnerability to widespread harvest pressure



Hon-Ki Chan a,*, Kevin T. Shoemaker b, Nancy E. Karraker a,1

- ^a School of Biological Sciences, The University of Hong Kong, Hong Kong, China
- ^b Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794, USA

ARTICLE INFO

Article history:
Received 28 August 2013
Received in revised form 8 December 2013
Accepted 10 December 2013

Keywords: Amphibian China Harvesting Population decline Population viability analysis Ouasinaa

ABSTRACT

Over 20 species of amphibians are being harvested in Asia with local consumption exceeding the volume of international export in some countries. Over-harvesting is a particular concern for large-bodied species as their life history traits often make them prone to population depletion. Quasipaa spinosa is a large, stream-dwelling frog that is considered a delicacy in China. The demand for its meat is high, with domestic trade amounting to USD 32 m in one province alone in one year. Although it is known that populations of Q. spinosa have been heavily depleted, no information on the demography of wild populations has been available to assess declines and vulnerability to ongoing exploitation. We studied Q. spinosa in Hong Kong, China, where populations are protected from hunting and habitat is largely unaltered. Results from a population viability analysis suggest that these populations are highly vulnerable to hunting activity; hunted populations were associated with much lower expected abundance and substantially higher risk of extirpation than populations free from harvesting pressure. Harvesting confers at least 59% reduction of abundance in 5 years. Based on ongoing harvesting of this species from the wild and our determination that relatively low levels of harvesting can lead to population extirpation in the short term, we call for the establishment of protection measures (State Protected Animal status) for this species throughout China and advocate for strengthened enforcement of existing regulations in nature reserves and other protected areas. Some currently harvested amphibians in China, including other species of Quasipaa, are probably similarly threatened by unregulated harvesting activities and we recommend that their status and vulnerability to harvesting be carefully reviewed.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Harvesting of wildlife has emerged as one of the most important global threats to vertebrate populations (Bennett et al., 2002; Hoffmann et al., 2010). Although a broad array of wildlife species are hunted, amphibians remain an important food resource in many countries. It is estimated that over one billion frogs are traded internationally every year to meet the demand for frogs' legs in the US and Europe, and especially in France and Belgium (Gratwicke et al., 2009; Mohneke et al., 2009; Altherr et al., 2011; Warkentin et al., 2009). Most frogs are imported from Southeast Asia, as France and India have banned collection of native frogs (Altherr et al., 2011). Nearly half of frogs traded internationally come from Indonesia (Gratwicke et al., 2009). Between 2000

and 2009, the European Union imported a total of 46,400 tons of frogs' legs mainly from Asia, which amounts to an average of 93-230 million frogs annually (Altherr et al., 2011). High demand for frog meat has severely depleted populations of multiple species worldwide (Jensen and Camp, 2003; Carpenter et al., 2007). Over 20 species are harvested on a commercial scale in Asia (Kusrini and Alford, 2006; Altherr et al., 2011), and populations of these species are declining as a result. For instance, of the 39 ranid frogs harvested in China, populations of 12 of them are considered to be rapidly declining (Carpenter et al., 2007). Two species from Asia are now listed on CITES Appendix II and 16 more were proposed for listing in 1992 (Altherr et al., 2011). Amphibians generally have short lifespans, high fecundity, and large population sizes. These life history features, in part, have prompted researchers to conclude that amphibians are resilient to harvesting (Lau et al., 2008), even though annual take of amphibians currently numbers in the hundreds of millions (Kusrini, 2005).

Although international trade of frog meat is well documented, the extent of amphibian take for local consumption remains understudied, and in some cases, the quantities harvested for local consumption may far exceed the quantities exported. For instance, it is

^{*} Corresponding author. Current address: Kadoorie Farm and Botanic Garden, Lam Kam Road, Tai Po, New Territories, Hong Kong. Tel.: +852 2483 7200; fax: +852 2488 6702.

E-mail address: honkichan@gmail.com (H.-K. Chan).

¹ Current address: Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881, USA.

estimated that the number of frogs harvested and consumed within Indonesia may be two to seven times the quantity exported (Kusrini, 2005). Similarly, revenues from global trade of frog meat has been estimated as USD 40 m annually (Gratwicke et al., 2009), yet domestic trade in China of a single species, the giant spiny frog (Quasipaa spinosa), is estimated to be USD 32 m in one year from a single province (Yu and Ma, 2012). Local consumption alone can severely deplete populations as has been reported in West Africa (Mohneke et al., 2009) and Peru (Angulo, 2008).

Populations of *Q. spinosa* are estimated to have declined by more than 30% over the past decade, likely as a consequence of overharvesting (Lau et al., 2004). This species is now listed as Vulnerable by the IUCN and the China Red List (Zhao, 1998; Lau et al., 2004). Despite ongoing population declines, the species has not been designated as a State Protected Animal by the Chinese Government, and thus there are no regulations for its protection except where prohibitions on collection are enforced within China's nature reserves. This species is an important food and medicinal resource in China, (Ye et al., 1993; Gao, 1996), and thus we sought to assess the impacts of harvesting on populations. In this paper, we quantify the demography and related aspects of the ecology of Q. spinosa populations in Hong Kong, and we present the first quantitative assessment of the population-level consequences of hunting and commercial harvest on this widely harvested amphibian species. We suggest that there is an urgent need for similar studies on other Asian amphibian species potentially threatened by overharvesting.

2. Materials and methods

2.1. Study sites

We studied populations of *Q. spinosa* in two streams in Tai Mo Shan Country Park, a protected area with minimal human disturbance. Stream A (750–850 m in elevation) and Stream B (600–700 m) were not connected. Tai Mo Shan, the tallest (960 m) mountain in Hong Kong, is characterized by steep slopes with high gradient streams. Surrounding vegetation is grassland and shrubland, with patches of montane forest in ravines.

2.2. Animal sampling

On each stream, we surveyed a 200-m transect. Transect locations were selected based on known occurrences of the species on each stream. Transect length was limited by sections of dangerously steep terrain that bounded locations of known occurrence. Surveys were conducted every one to two months from September 2009 through July 2012, which included wet (May to October) and dry (November to April) seasons. Two to three surveyors walked upstream, one hour after dark, searching for frogs. All *Q. spinosa* large enough to be marked (snout-vent length, SVL \geqslant 40 mm)

were captured. We recorded SVL (mm), weight (g), sex (males have keratinized spines on chest and fingers), and location of frogs on transects. Frogs were classified as unsexed juveniles (40 mm \leq SVL \leq 89 mm) or adults (SVL \geq 90 mm) (Liu et al., 1990). Each new individual was injected with a passive integrated transponder tag (Biomark, Boise, Idaho, US). Recaptured frogs were identified by scanning the frog with a tag reader. We recorded search time for each survey, and search effort was standardized among surveys.

2.3. Population vital rates

We used Cormack–Jolly–Seber (CJS) models to estimate annual survival (ϕ) and recapture probability (ρ), and closed population models (jackknife estimator; Burnham and Overton, 1978) to estimate annual abundances (N). Survey data were pooled into threemonth intervals, resulting in 12 pooled survey bouts over the three-year study. Abundance was estimated separately for the two populations, and data from the two sites were pooled for survival estimation. Sex/age class (adult male, adult female and juvenile), survey bout, study population and season were included as covariates in the candidate CJS model set for modeling survival (ϕ) and capture probability (p). Of those models for which all parameters were uniquely estimable, the five models with lowest AlC_c were retained for model averaging (Burnham and Anderson, 2002). All analyses were performed using Program Mark 7.1 (White and Burnham, 1999).

2.4. Population viability analysis

Population viability analysis (PVA) was conducted to assess the vulnerability of O. spinosa to hunting activity. Biological parameters for PVA were based on Fei et al. (2009) and this study. Models were run for 100 years, and risk was summarized as the percentage of simulation replicates that were extirpated. Capture efficiency of adults for each survey (subsequently used for assessing harvest impacts) was estimated as the number of adults captured per survey bout expressed as a proportion of total estimated abundance at each stream. Harvest was modeled as the annual removal of mature individuals by a single collector assuming either (1) moderate capture efficiency (mean capture efficiency based on abundance estimates; hereafter, moderate hunting scenario) or (2) high capture efficiency (95% confidence limit of capture efficiency based on abundance estimates; hereafter, intense hunting scenario). To test the population-level impacts of harvest while accounting for substantial parameter uncertainty, six scenarios were created, comprising all possible combinations of three harvest scenarios (no hunting, moderate hunting, intense hunting) and two recruitment scenarios (moderate recruitment and high recruitment). Moderate recruitment was estimated as the expected juvenile abundance (via jackknife estimator, averaged across the two study sites) in year t, divided by the expected abundance of reproductive

Table 1 Cormack–Jolly–Seber model estimates of apparent survival (ϕ) for *Quasipaa spinosa* in two streams in Hong Kong, China.

Site	Season	ϕ	SE	95% CI	Estimated by
Stream A	Annual	0.434	0.053	0.335-0.540	$\phi(\text{site})p(t)$
	Dry	0.441	0.098	0.265-0.632	$\phi(\text{season} * \text{site})p(t)$
	Wet	0.428	0.125	0.216-0.670	$\phi(\text{season} * \text{site})p(t)$
Stream B	Annual	0.696	0.073	0.538-0.818	$\phi(\text{site})p(t)$
	Dry	0.940	0.154	0.075-0.999	$\phi(\text{season} * \text{site})p(t)$
	Wet	0.476	0.133	0.242-0.720	$\phi(\text{season} * \text{site})p(t)$
Overall	Annual	0.518	0.048	0.424-0.609	$\phi(\text{site})p(t)$
	Dry	0.552	0.799	0.336-0.750	Models averaged
	Wet	0.492	0.064	0.345-0.640	Models averaged

Table 2 Population sizes (*N*) of *Quasipaa spinosa* in two streams in Hong Kong, China, estimated via the closed-population jackknife estimator.

Year	Sex/age class	N (SE)	95% CI
Stream A			
September 2009-August 2010	Male adult	24 (3.94)	20-37
	Female adult	16 (2.74)	15-29
	Juvenile	43 (7.70)	33-63
September 2010-August 2011	Male adult	20 (3.25)	17-32
	Female adult	43 (7.15)	34-63
	Juvenile	20 (4.04)	16-33
September 2011–July 2012	Male adult	13 (3.69)	9-25
	Female adult	23 (5.63)	17-40
	Juvenile	16 (3.01)	14-28
Stream B			
September 2009-August 2010	Male adult	8 (1.17)	8-13
	Female adult	19 (2.03)	18-27
	Juvenile	Not estimated due to no capture	
September 2010-August 2011	Male adult	5 (2.19)	5-20
	Female adult	16 (2.62)	15-29
	Juvenile	5 (1.17)	5–10
September 2011–July 2012	Male adult	6 (2.13)	4-13
	Female adult	14 (3.69)	11-26
	Juvenile	28 (6.36)	20-46

females in year t-2. For high recruitment scenarios, we used the upper limit of the 95% confidence limit of juvenile abundance in place of mean juvenile abundance. We also computed a low recruitment scenario (using the lower limit of the 95% confidence interval for juvenile abundance), but this scenario resulted in rapid extinction for all scenarios tested and was not considered further. All PVAs were conducted in Vortex 9.99 (Lacy et al., 2010). Population-level risk due to harvest was computed as (1) percent reduction in abundance at year 5 (before populations were extirpated under any harvest scenario) relative to a no harvest scenario, and

(2) absolute decrease in time (years) to extirpation relative to a no harvest scenario. Parameters are listed in Table 3.

2.5. Movement patterns and territoriality

For frogs encountered more than once, territory size was estimated as the distance between the two farthest locations of capture. As stream channels were relatively confined and *Q. spinosa* are highly aquatic, territories were calculated as linear distance rather than area. Differences in territory size between sites and

Table 3Estimated values of parameters used in population viability analysis assessing the impacts of hunting on *Quasipaa spinosa* populations in Hong Kong, China.

Category	Parameters	Value	Reference
Scenario settings	No. of iterations No. of years Extinction definition No. of populations	100 100 1 Sex remains 2	- - - -
Dispersal	Dispersal between populations	Negligible	This study
Reproductive systems	Mating system Age of first offspring Max. age of reproduction Max. number of broods per year	Polygynous 1 years, both sexes 10 1	Fei et al. (2009) - Presumed Multiple clutches laid within a short breeding period (Fei et al., 2009)
	% Male at birth	50	Presumed
Reproductive rate	% Of adult female breeding Mean # juveniles per female per year	100 Moderate = 1.26	Presumed Closed population models of this study (Table 2)
Mortality rate	Mortality rate	High = 2.11 48.2% For both sexes and all age classes	Open population models of this study (Table 1)
Mate monopolization	% Males in breeding pool	100	Presumed
Initial population size	Initial population size	Stream A = 83 Stream B = 48	Closed population models of this study (Table 2)
Carrying capacity	Carrying capacity (abundance ceiling)	150	Presumed
Harvest	Harvest year and interval Harvest capture efficiency	Year 1-15, harvest annually Moderate hunting Stream A = 16.5% Stream B = 24.3% Intense hunting Stream A = 27.4% Stream B = 44.2%	Presumed This study (Fig. 1)

sexes were tested separately with a Mann-Whitney U test. We assumed the center of a territory to be the average of locations where a frog was captured.

3. Results

We conducted 24 surveys on Stream A and 23 on Stream B and marked 141 individual *Q. spinosa* (98 from Stream A; 43 from Stream B; Fig. 1). Migration of individuals between two streams was never observed during the three year survey period.

3.1. Population vital rates

Mean annual survival for *Q. spinosa* was 0.518 (95% CI: 0.424 – 0.609) and was influenced strongly by site, although some effects of seasonality were apparent. Annual survival was higher in Stream B (0.696) than in Stream A (0.434). Mean survival rates were similar between dry (0.552) and wet seasons (0.492). Our best model (ϕ (season * site)p(t); Table 1) suggested that the population in Stream B had a higher survival rate than that in Stream A in dry seasons (Stream B: 0.940 vs. Stream A: 0.441), but that survival rates were similar during wet seasons (Stream B: 0.476 vs Stream A: 0.428). However, these estimates should be interpreted with caution, given the large associated sampling error (Table 1).

From the closed population model, we estimated that Stream A had a larger population density of 40–129 frogs per 200 m of stream, compared with 25–82 in Stream B (Table 2, Fig. 2). Abundance and demographic structure (age class and sex ratios) varied substantially among years (Fig. 2). Sex ratio was skewed in Stream A (male ratio = 0.32–0.36; χ^2 = 6.39, df = 2, P = 0.041) and Stream B (male ratio = 0.24–0.30; χ^2 = 6.72, df = 2, P = 0.035). Sex ratio was skewed when we combined the data from the two streams (male ratio = 0.30–0.48; χ^2 = 9.84, df = 2, P = 0.007).

3.2. Population viability analysis

Estimated recruitment rate for *Q. spinosa* was 1.26 (moderate) to 2.11 (high) juveniles per female (Table 3). At moderate

recruitment rates, hunting resulted in a 60% (moderate hunting) to 80% (intense hunting) decrease in expected abundance (year 5) at Stream A and a 72% to 92% decrease in expected abundance at Stream B. Hunting decreased the expected time to extirpation by 8-12 years for Stream A and 7-11 Stream B, relative to a no hunting scenario. At high recruitment rates, hunting resulted in a 59% (moderate hunting) to 78% (intense hunting) decrease in expected abundance (year 5) in Stream A and a 75 to 95% decrease in expected abundance in Stream B. relative to a no harvest scenario. The high-recruitment and no harvest scenario was associated with long-term population stability (probability of persistence >0.99 at year 100) in both streams. However, moderate harvest rates were sufficient to destabilize both populations, resulting in potential extirpation (abundance below two individuals) in Stream A at year 35 (0.82 probability of extirpation and 99% reduction in abundance) and Stream B at year 17 (0.68 probability of extirpation and 99% reduction in abundance).

3.3. Movement patterns and territoriality

We captured 67% (32 males, 49 females) of individuals more than once and determined that long-distance movements were rare. The species appears to be territorial with most (89%) individuals (28 males, 44 females) being observed in the same location and exhibiting relatively small territory sizes, averaging 11.7 linear meters (median = 10 m, range = 0-42 m). Nine individuals (11%; 4 males and 5 females) moved 67-183 m up- or downstream after being repeatedly captured in the original location. As these nine individuals moved substantial distances from their original locations, they were not included in the territory size analysis. For the 72 individuals that remained in relatively the same location, territory sizes did not differ between sexes $(U_{(2)28.44} = 565.5, P = 0.559)$ but differed between sites $(U_{(2)23.49} = 357.5, P = 0.013)$. Frogs in Stream B had larger territory sizes (n = 23, mean = 16.4, SE = 2.23) than those in Stream A (n = 49, mean = 10.26, SE = 1.16).

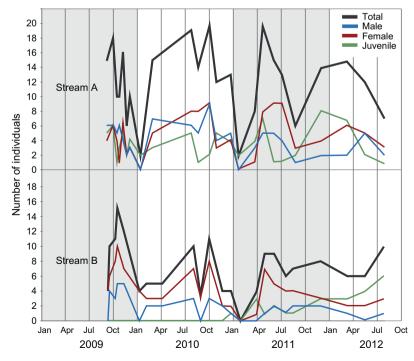


Fig. 1. Number of Quasipaa spinosa captured in each survey in Hong Kong, China.

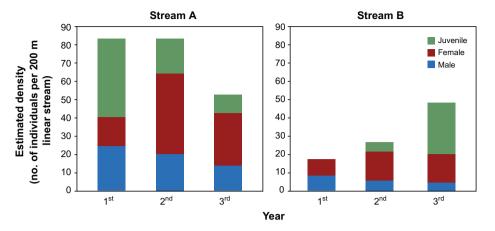


Fig. 2. Estimated density of Quasipaa spinosa by year in two streams in Hong Kong, China.

4. Discussion

Q. spinosa exhibits particular biological and ecological traits, including large body size, stream-breeding, and a restricted geographical range due to habitat requirements, that make it highly vulnerable to population declines associated with human-induced stressors such as harvesting, as has been shown in other frog species (Green, 2003; Lips et al., 2003; Xie et al., 2007; Sodhi et al., 2008). For Q. spinosa, population densities are low and annual recruitment is apparently low, potentially predisposing populations to declines. Indeed, our population viability analysis indicated that these populations are highly vulnerable to harvesting. In other parts of China, Quasipaa species are heavily harvested, and especially Q. spinosa, which is considered a delicacy. Demand for *Quasipaa* frogs is reflected in their soaring price, which has increased from USD 2/kg in the 1980s to 10-30/kg today (Yu and Ma, 2012; H-K Chan, pers. obs.). Although global trade of frog meat amounts to USD 40 m annually (Gratwicke et al., 2009), Jiangxi Province alone produced USD 32 m worth of O. spinosa products for domestic consumption in 2011 (Yu and Ma, 2012). Thus, trading of Quasipaa represents a multimillion-dollar industry in China. There are large-scale frog farms producing Q. spinosa for commercial sale, but most are located within protected areas and usually operate with permission from the local government, whether lawful or not. With only sporadic reports of successful captive breeding and commercial-scale production largely unproven, "farmed" frogs are most likely sourced from tadpoles or adults harvested from the wild. Farming of Q. spinosa is hampered by low fertilization and hatching rates, disease, high overwinter mortality, and inbreeding depression (Yu and Ma, 2012; Liang et al., 2013). Frog farms still rely heavily on wild frogs as breeding stock (Liang et al., 2013). Even if frog farming is successful to some extent, it poses risk of disease and genetic pollution to wild populations (Mockrin et al., 2005), as frog farms are usually located near natural habitats (Liang et al., 2013). Farming of wildlife for trade may not necessarily reduce hunting pressure on wild populations as wild-caught animals can be "laundered" as captive-bred through farms, as has been reported in many other species (e.g. Nijman and Shepherd, 2009; Lyons and Natusch, 2011).

We determined that abundance and probability of persistence declined substantially if populations were hunted by a single person on a single occasion per year (Fig. 3). However, actual hunting pressure in the field is potentially more severe as populations may be hunted multiple times per year by multiple hunters. Consequently, many populations accessible to hunters may already have been extirpated. The extent and impact of hunting on wild *Q*.

spinosa populations in China should be more thoroughly investigated, and a higher IUCN risk classification may be warranted for this species, given our results.

In addition to harvesting, *Q. spinosa* in China face multiple threats to their habitats including pollution from upland agriculture and habitat degradation by dam and hydropower projects. An assessment of the importance of these impacts has not been undertaken, but it is likely that these factors, and the latter in particular, are eroding populations. Population losses and needed protections are also confounded by a lack of resolution on the evolutionary relationships among populations. A recent phylogenetic study suggested that *Q. spinosa* may be a cryptic species complex that includes at least three evolutionarily-independent candidate species (Che et al., 2009). Since individual cryptic species will have smaller ranges than the entire species complex, species separated from this complex are likely to be classified in a higher IUCN Red List risk category than as the complex is currently listed.

We found that Q. spinosa exhibits high site fidelity, with some individuals being found in similar locations in successive years. Several stream frogs have been documented as philopatric (Inger, 1969; Kam and Chen, 2000; Robertson et al., 2008), and this is presumably related to the patchy distribution of resources, including suitable oviposition, retreat, and calling sites. Although we observed that 10% of frogs moved more than 50 m from their original location, these movements were not considered seasonal breeding migrations because frogs remain in the streams year-round and the movements we documented had no systematic element to them in terms of time or space. Q. spinosa tended to move in an upstream direction, despite the steep gradient and large substrates in some sections of the streams. Stream slope may present a dispersal barrier for amphibians (Lowe et al., 2006), and upstream populations can be denuded over time by downstream larval drift with peak discharge during the monsoon season. This occasional upstreambiased movement behavior may be critical to compensate for downstream larval drift, as has been documented in the dispersal patterns of aquatic invertebrates (Müller, 1982) and some amphibians (Lowe, 2003; Robertson et al., 2008), and may maintain gene flow between upstream and downstream populations (Robertson et al., 2008).

Dispersal (i.e., immigration and emigration from our study sites) was not observed in this study and is assumed to be low or non-existent by closed population mark-recapture and PVA models. Failure to account for dispersal in closed population models can produce survival estimates that are biased low (Hines et al., 2003), because animals no longer detected in a population are assumed to have died rather than emigrated. For this reason, actual survival rates and population persistence probabilities may be

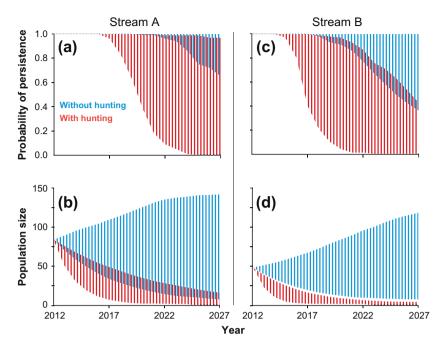


Fig. 3. Probability of population persistence (a and c) and population size (b and d) for *Quasipaa spinosa* at two survey sites in Hong Kong, China over the next 15 years, based on population viability analysis. For scenarios without hunting, cross-hatched areas are bounded by scenarios of high (upper bound) and moderate (lower bound) recruitment. For hunted scenarios, cross-hatched areas are bounded by scenarios of high recruitment with moderate hunting (upper bound) and moderate recruitment with intense hunting (lower bound).

higher than those estimated in this study. However, small biases in model parameters are unlikely to reverse the strong impacts of harvesting estimated in this study (Reed et al., 2002). In fact, the population-level impact of harvesting of adults tends to be magnified for species with higher adult survival rates (e.g., Crowder et al., 1994).

Our model estimated high apparent survival in the dry season for *Q. spinosa* in Stream B (Table 1). We note that this estimate is based on limited data and therefore the sampling uncertainty is also extremely high. As the confidence interval for this estimate overlaps with the confidence intervals for wet season and overall survival, it is possible that this high estimate for dry season survival is an artifact of sampling uncertainty and not a reflection of an extremely high survival rate during the dry season.

Q. spinosa exhibited a population density ranging from 26 to 83 frogs per 200 m of stream. This density is comparable with that of Craugastor punctariolus, a large-sized, montane stream frog, which exhibited a density of 19-68 individuals per 200 m of stream in Panama (Ryan et al., 2008). The estimated annual survival (0.43-0.70) of Q. spinosa is considerably lower than that of C. punctariolus (0.87-0.94; Ryan et al., 2008) and the salamander Dicamptodon tenebrosus from North America (0.76-0.90; Sagar et al., 2007). Annual survival in Q. spinosa is comparable with that of the frog Mixophyes fleayi (0.38-0.65) from Australia (Newell et al., 2013). Relatively low survival in Q. spinosa may result from skewed survival among individuals in the population, whereby a few individuals may be better able to secure territories and associated resources. However, we were not able to detect differences in survival rate among individuals because of sources of heterogeneity such as body size.

Sex ratio was female-biased throughout the study, contradicting the observation (Wells, 2007) that amphibians exhibiting male-male competition often have male-biased sex ratios. Shifts in sex ratios from male- to female-biased may be a symptom of a declining population (Lips, 1998). However, this is not likely the case for our populations as there have been no observed amphibian declines in the area. Female-biased sex ratios may also result from

male-biased mortality (e.g. Denton and Beebee, 1993). Our population models indicated neither sex-specific mortality nor sex-specific recapture probability. However, we only marked individuals \geqslant 40 mm. Therefore, if male-biased mortality is affecting the sex ratio it must be occurring before frogs reach 40 mm in size, but there is little reason to suspect that sex-biased mortality would be occurring in sexually immature individuals.

Tremendous market demand continues to sustain illegal hunting by local people in China outside of Hong Kong (Fei et al., 2009; Yu and Ma, 2012). We suspect that hunting threatens most accessible frog populations because individual hunters can collect relatively large numbers of frogs on a single night and there has been limited enforcement of regulations in many protected areas in China. News reports on confiscations of illegally hunted Q. spinosa in China often involve 100-500 animals in each operation (Anon, 2004a,b). We estimated natural densities to be 50 frogs per 200 of stream in our study. Reported confiscations of hundreds of Q. spinosa suggests the harvest of large numbers from previously unexploited populations, the chronic removal of fewer individuals from already depleted populations, or, most likely, some combination of the two. As broad-scale surveys of Q. spinosa populations have not been conducted outside of Hong Kong, it is not known if relatively intact populations exist that should be targeted for increased protection. However, such information, if acted upon, could yield significant conservation benefits for the species.

The Fujian Provincial Department of Forestry has recently begun to regulate trade in *Q. spinosa*. Sales from wild sources are now banned in Fujian Province and captive frogs must be officially certified. Accordingly, frog farms in Fujian Province are monitored and the introduction of wild individuals for captive breeding purposes is now regulated. It is not known at this time if these regulations are strictly enforced, but these efforts may help to reduce harvesting from wild populations there.

Our study delineates the demography of *Q. spinosa* populations in Hong Kong and clearly demonstrates that hunting poses considerable risk to the long-term viability of populations. We emphasize that there is little evidence that captive breeding

for commercial-scale farming of *Q. spinosa* has been successful and "farmed" frogs are most likely sourced from tadpoles or adults collected from wild populations. Based on ongoing overexploitation of this species and our finding that relatively low levels of harvesting can lead to population extirpation in a short period of time, we strongly advocate that *Q. spinosa* be listed as a State Protected Animal in China and call for strengthened enforcement of existing regulations in protected areas. We propose that other harvested frogs in Asia, such as *Quasipaa verrucospinosa*, *Fejevarya cancrivora*, and *Limnonectes macrodon*, may be similarly at risk and that the vulnerability of these species should also be carefully reviewed.

Acknowledgements

We thank T.C. Lau, A.C.Y. Yeung, W.I. Chung, C.Y. Ma, X. Niu and Y.H. Sung for assistance in the field; D. Dudgeon for logistical support and helpful suggestions; E.J. Pickett for comments on the manuscript; and C.Y. Ng for technical support. We are grateful to J.E. Nichol and M.S. Wong for granting access to their GIS habitat data. This project was funded by the University Grants Committee in Hong Kong and was approved by the University of Hong Kong Committee on the Use of Live Animals in Teaching and Research (permit #1830-09) and the Hong Kong Department of Health (Animals Ordinance permit # 09-692). K.T. Shoemaker was supported by NSF Grant DEB-1146198.

References

- Altherr, S., Goyenechea, A., Schubert, D., 2011. Canapés to extinction: The international trade in frogs' legs and its ecological impact. Pro Wildlife, Defenders of Wildlife, Animal Welfare Institute. Munich, Germany; Washington D.C., USA.
- Angulo, A., 2008. Consumption of Andean frogs of the genus *Telmatobius* in Cusco, Peru: recommendations for their conservation. TRAFFIC Bull. 21, 95–97.
- Anon, 2004a. Eight hunters arrested in a night police action. Jianghuai Morning Post. http://news.sina.com.cn/c/2004-09-06/00363590534s.shtml (accessed 23.11.13) (in Chinese).
- Anon, 2004b. Five hundred illegally collected spiny frogs released in Meizhou. Shantou City Daily. http://news.sina.com.cn/s/2004-11-29/11194379309s.shtml (accessed 23.11.13) (in Chinese).
- Bennett, E., Milner-Gulland, E., Bakarr, M., Eves, H., Robinson, J., Wilkie, D., 2002. Hunting the world's wildlife to extinction. Oryx 36, 328–329.
- Burnham, K.P., Anderson, D., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second ed. Springer-Verlag, New York
- Burnham, K.P., Overton, W.S., 1978. Estimation of the size of a closed population when capture probabilities vary among animals. Biometrika 65, 625–633.
- Carpenter, A.I., Dublin, H., Lau, M., Syed, G., McKay, J.E., Moore, R.D., 2007. Overharvesting. In: Gascon, C., Collins, J.P., Moore, R.D., Church, D.R., McKay, J.E., Mendelson, J.R., III (Eds.), Amphibian Conservation Action Plan. IUCN, Gland, Switzerland.
- Che, J., Hu, J.S., Zhou, W.W., Murphy, R.W., Papenfuss, T.J., Chen, M.Y., Rao, D.Q., Li, P.P., Zhang, Y.P., 2009. Phylogeny of the Asian spiny frog tribe Paini (Family Dicroglossidae) sensu Dubois. Mol. Phylogenet. Evol. 50, 59–73.
- Crowder, L.B., Crouse, D.T., Heppell, S.S., Martin, T.H., 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle population. Ecol. Appl. 4, 437– 445.
- Denton, J.S., Beebee, T.J.C., 1993. Reproductive strategies in a female-biased population of natterjack toads, *Bufo calamita*. Anim. Behav. 46, 1169–1175.
- Fei, L., Hu, S., Ye, C., Huang, Y., 2009. Fauna Sinica. Amphibia, vol. 3. Science Press, Beijing, China (in Chinese).
- Gao, S., 1996. Zhongguo dong wu yao zhi (Record of Chinese Animal Materia Medica). Jilin Science and Technology Press, Jilin (in Chinese).
- Gratwicke, B., Evans, M.J., Jenkins, P.T., Kusrini, M.D., Moore, R.D., Sevin, J., Wildt, D.E., 2009. Is the international frog legs trade a potential vector for deadly amphibian pathogens? Front. Ecol. Environ. 8, 438–442.
- Green, D.M., 2003. The ecology of extinction: population fluctuation and decline in amphibians. Biol. Conserv. 111, 331–343.
- Hines, J.E., Kendall, W.L., Nichols, J.D., 2003. On the use of the robust design with transient capture–recapture models. Auk 120, 1151–1158.
- Hoffmann, M., Hilton-Taylor, C., Angulo, A., Bohm, M., Brooks, T., Butchart, S., Carpenter, K., Chanson, J., Collen, B., Cox, N., 2010. The impact of conservation on the status of the world's vertebrates. Science 330, 1503–1509.

- Inger, R.F., 1969. Organization of communities of frogs along small rain forest streams in Sarawak. J. Anim. Ecol. 38, 123–148.
- Jensen, J.B., Camp, C.D., 2003. Human exploitation of amphibians: direct and indirect impacts. In: Semlitsch, R.D. (Ed.), Amphibian Conservation. Smithsonian Institution, Washington, pp. 199–213.
- Kam, Y.C., Chen, T.C., 2000. Abundance and movement of a riparian frog (*Rana swinhoana*) in a subtropical forest of Guandau stream, Taiwan. Zoological Stud. 39, 67–76.
- Kusrini, M.D., 2005. Edible frog harvesting in Indonesia: evaluating its impact and ecological context. PhD dissertation, James Cook University, Townsville, Australia.
- Kusrini, M.D., Alford, R.A., 2006. Indonesia's export of frogs' legs. Traffic Bull. 21, 13–
- Lacy, R.C., Borbat, M., Pollak, J.P., 2010. Vortex: A Stochastic Simulation of the Extinction Process. Chicago Zoological Society, Brookfield, IL, USA.
- Lau, M.W.N., Geng, B., Gu, H., van Dijk, P.P., Bain, R., 2004. Quasipaa spinosa, in: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. www.iucnredlist.org.
- Lau, M., van Dijk, P.P., Syed, G.P., 2008. Managing problems of over-exploitation and trade in amphibians. In: Stuart, S., Hoffmann, M., Chanson, J., Cox, N., Berridge, R., Ramani, P., Young, B. (Eds.), Threatened Amphibians of the World. Lynx Edicions. Barcelona.
- Liang, Z., Xu, Q., Jiang, Y., Qin, J., Deng, W., 2013. Situation and development of Quasipaa spinosa in Yongfu County. Guangxi Anim. Husbandry Veterinary Med. 29 (4), 244–246 (in Chinese).
- Lips, K.R., 1998. Decline of a tropical montane amphibian fauna. Conserv. Biol. 12, 106–117.
- Lips, K.R., Reeve, J.D., Witters, L.R., 2003. Ecological traits predicting amphibian population declines in Central America. Conserv. Biol. 17, 1078–1088.
- Liu, Y., So, X., Li, R., Huang, X., Lu, Y., 1990. Study of gonad development on *Quasipaa spinosa*. Fujian Fisheries 2, 15–24 (in Chinese).
- Lowe, W.H., 2003. Linking dispersal to local population dynamics: a case study using a headwater salamander system. Ecology 84, 2145–2154.
- Lowe, W.H., Likens, G.E., McPeek, M.A., Buso, D.C., 2006. Linking direct and indirect data on dispersal: Isolation by slope in a headwater stream salamander. Ecology 87, 334–339.
- Lyons, J.A., Natusch, D.J.D., 2011. Wildlife laundering through breeding farms: Illegal harvest, population declines and a means of regulating the trade of green pythons (*Morelia viridis*) from Indonesia. Biol. Conserv. 144, 3073–3081.
- Mockrin, M.H., Bennett, E.L., LaBruna, D.T., 2005. Wildlife farming: A viable alternative To hunting in tropical forests? In WCS Working Paper No. 23. Wildlife Conservation Society, New York.
- Mohneke, M., Onadeko, A.B., Rödel, M.-O., 2009. Exploitation of frogs a review with a focus on West Africa. Salamandra 45 (4), 193–202.
- Müller, K., 1982. The colonization cycle of freshwater insects. Oecologia 52, 202–207.
- Newell, D.A., Goldingay, R.L., Brooks, L.O., 2013. Population recovery following decline in an endangered stream-breeding frog (*Mixophyes fleayi*) from subtropical Australia. PLoS ONE 8, e58559.
- Nijman, V., Shepherd, C.R., 2009. Wildlife trade from ASEAN to the EU: Issues with the trade in captive-bred reptiles from Indonesia. In TRAFFIC Europe Report for the European Commission. Brussels. Belgium.
- Reed, J.M., Mills, L.S., Dunning, J.B., Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M.-C., Miller, P., 2002. Emerging issues in population viability analysis. Conserv. Biol. 16, 7–19.
- Robertson, J.M., Lips, K.R., Heist, E.J., 2008. Fine scale gene flow and individual movements among subpopulations of *Centrolene prosoblepon* (Anura: Centrolenidae). Rev. Biol. Trop. 56, 13–26.
 Ryan, M.J., Lips, K.R., Eichholz, M.W., 2008. Decline and extirpation of an
- Ryan, M.J., Lips, K.R., Eichholz, M.W., 2008. Decline and extirpation of an endangered Panamanian stream frog population (*Craugastor punctariolus*) due to an outbreak of chytridiomycosis. Biol. Conserv. 141, 1636–1647.
- Sagar, J.P., Olson, D.H., Schmitz, R.A., Beaupre, S.J., 2007. Survival and growth of larval coastal giant salamanders (*Dicamptodon tenebrosus*) in streams in the Oregon Coast Range. Copeia 2007, 123–130.
- Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H., Bradshaw, C.J.A., 2008. Measuring the meltdown: drivers of global amphibian extinction and decline. PLoS ONE 3 (2), e1636.
- Warkentin, I.G., Bickford, D., Sodhi, N.S., Bradshaw, C.J.A., 2009. Eating frogs to extinction. Conserv. Biol. 23, 1056–1059.
- Wells, K.D., 2007. The Ecology and Behavior of Amphibians. University of Chicago Press, Chicago, IL.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, 120–139.
- Xie, F., Lau, M.W.N., Stuart, S.N., Chanson, J.S., Cox, N.A., Fischman, D.L., 2007. Conservation needs of amphibians in China: a review. Sci. China Ser. C: Life Sci. 50, 265–276.
- Ye, C., Fei, L., Hu, S., 1993. Rare and Economic Amphibians of China. Sichuan Publishing House of Science and Technology, Chengdu (in Chinese).
- Yu, Z., Ma, B., 2012. Status of the *Quasipaa spinosa* industry in Jiangxi. Jiangxi Shuichan Keji 2, 4–8 (in Chinese).
- Zhao, E., 1998. China Red Data Book of Endangered Animals Amphibia. Science Press, Beijing (in Chinese).