POLICY PERSPECTIVE

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Widespread occurrence of an emerging fungal pathogen in heavily traded Chinese urodelan species

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Abstract

Understanding introduction routes for wildlife pathogens is vital for the development of threat abatement plans. The chytrid fungus *Batrachochytrium salamandrivorans* (Bsal) has recently emerged in Europe, where it is considered to be a serious threat for urodelan conservation. If the highly diverse Chinese urodelans were to constitute a Bsal reservoir, then the significant international trade in these species may vector Bsal into naïve urodelan communities. Here, we analyzed a total of 1,143 samples, representing 36 Chinese salamander species from 51 localities across southern China for the presence of Bsal. We found Bsal was present across a wide taxonomic, geographical, and environmental range. In particular, Bsal DNA was detected in 33 samples from the genera *Cynops*, *Pachytriton*, *Paramesotriton*, *Tylototriton*, and *Andrias*, including the heavily traded species *Paramesotriton hongkongensis* and *Cynops orientalis*. The true Bsal prevalence across our data set was estimated between 2% and 4%, with a maximum of 50% in a population of *P. hongkongensis*. Even at this overall relatively low Bsal prevalence, the exportation of millions of animals renders Bsal introduction in naïve, importing countries a near certainty, which calls for the urgent implementation of proper biosecurity in the international wildlife trade.

KEYWORDS
Batrachochytrium salamandrivorans, biosafety, China, pet trade, salamander

1 | INTRODUCTION

Emerging fungal diseases are major drivers of global amphibian diversity loss (Fisher et al., 2012). Understanding pathways of pathogen introduction is key in shaping policy decisions aimed at the prevention of spillover into naïve regions. The chytrid fungus *Batrachochytrium salamandrivorans* (Bsal) recently invaded northwestern Europe (Martel et al., 2013), causing extinction events in urodelan populations (Stegen et al., 2017) and threatening the majority of urodelan diversity in the western Palearctic (Martel et al., 2014). Current evidence suggests Bsal is probably absent from the highly urodelan diverse regions in Northern and Latin America (Bales et al., 2015; Martel et al., 2014). In Asia, Bsal appears to coexist with native urodelan communities in Vietnam (Laking et al. 2017), Thailand, and Japan (Martel et al., 2014). This has led to the hypothesis that Bsal coevolved with Asiatic urodelans and has been vectored into Europe on live amphibians through the pet trade (Martel et al., 2014).

The large-scale harvest of Asian urodelans for trade has been shown to drive declines in at least some species (Rowley et al., 2016). Chinese species dominate this trade, with high numbers of specimens from the genera *Cynops*, *Pachytriton*, *Tylototriton*, and *Paramesotriton* having been traded over the past decades. For the United States alone, pet trade imports from China have included over 2.3 million specimens of *Cynops orientalis* during the period 2001-2009 (Herrel & Der Meijden, 2014) and an estimated over 300,000 specimens of *Paramesotriton hongkongensis* during the period 2005-2010 (Lee, Lau, & Chan, 2004; Xie et al., 2007). To date, firm evidence for the potential of Chinese species as vectors for Bsal is lacking and the only study performed on Chinese amphibians did not demonstrate the presence of the pathogen in Chinese amphibian communities (Zhu et al., 2014). However, only a limited number of salamanders (16 samples of *Andrias davidianus* and 19 samples of *C. orientalis*, which were from farms or food markets) were tested by Zhu et al. (2014). Given the volume of trade originating from China, conclusive evidence of Bsal presence on widely traded Chinese urodelans would further reinforce the need to speed up decision processes in the European Union and to strengthen existing trade bans in the United States and Canada. Moreover, quantifying the prior belief about the probability of presence and prevalence of the pathogen is key to devising effective biosecurity control and surveillance monitoring (Runge et al., 2017).

Here, we present this evidence, obtained from a large-scale field sampling for Bsal in Chinese urodelans, including the most widely traded salamandrid genera, which demonstrates presence of Bsal in several trade species, and remarkably high prevalence in some of them. These findings support urgent calls for immediate actions to restrict trade in live amphibians in order to prevent pathogen pollution and potential massive biodiversity loss.

2 | MATERIALS AND METHODS

Noninvasive skin samples were collected from Chinese salamander species belonging to the Salamandridae across the Chinese territory using cotton tipped swabs (Classical Swab, Copan Diagnostics, Brescia, Italia) between August 2016 and August 2017. In total, 51 localities were surveyed, seeking to broadly encompass the distributions of Chinese Salamanders (Figure 1). Most animals sampled were wild, except for 16 Chinese giant salamanders (*A. davidianus*) that were farm-bred. To avoid cross-contamination, gloves were changed each time after handling and sampling an animal and before catching a new individual. Swabs were stored at -20°C. Water and air temperatures were measured at each site upon collection of the first salamander in the sample.

The presence of Bsal in the swab samples was determined using simplex qPCR as described by Blooi et al. (2014). Briefly, genomic DNA was extracted from the swabs using 100 μl of Prepman Ultra reagent (Applied Biosystems, Foster City, CA), following the DNA extraction method described by Hyatt et al. (2007). We used a specific real-time PCR procedure described by Blooi et al. (2015) on CFX96 real-time system (Bio-Rad Laboratories, Hercules, CA). Genomic equivalents (GE) of Bsal zoospores were calculated per swab sample. Samples were run in duplicate and were considered positive based on a combination of: (1) shape of amplification curves (2) positive results in both duplications, and (3) returning GE values above the detection threshold. All positive samples were confirmed using sequencing of the amplicons.

In addition to the sample prevalence (the number of positive individuals in each sample), we sought to obtain estimates of the true prevalence in the sampled population, accounting for the uncertainty determined by the variable sample sizes. We assumed the number n of infected individuals out of a sample of size N to be a binomially distributed random variable $n \sim Bin(p, N)$, where p is the true prevalence of infection in the sampled population. This estimate provides a more realistic representation of our current knowledge of Bsal prevalence, and can, for example, be used as a prior belief for the design of surveillance monitoring and biosecurity controls. We estimated the average true prevalence across the entire data set, as well as true prevalence at the species, genus, and province level. We implemented the estimation in a Bayesian framework, using the JAGS software (Plummer, 2005). We used uninformative beta-distributed priors for p at all levels (overall, species, genus, and province), and drew 100,000 samples from three separate Markov chains after a burn-in of 50,000 iterations. We assessed convergence by visual inspection of the chain histories and using the R-hat statistic, and summarized estimates using the mean and 95% credible intervals (CRI) of the posterior distribution of p. Finally, we used logistic regression to model p across the entire data set as a linear
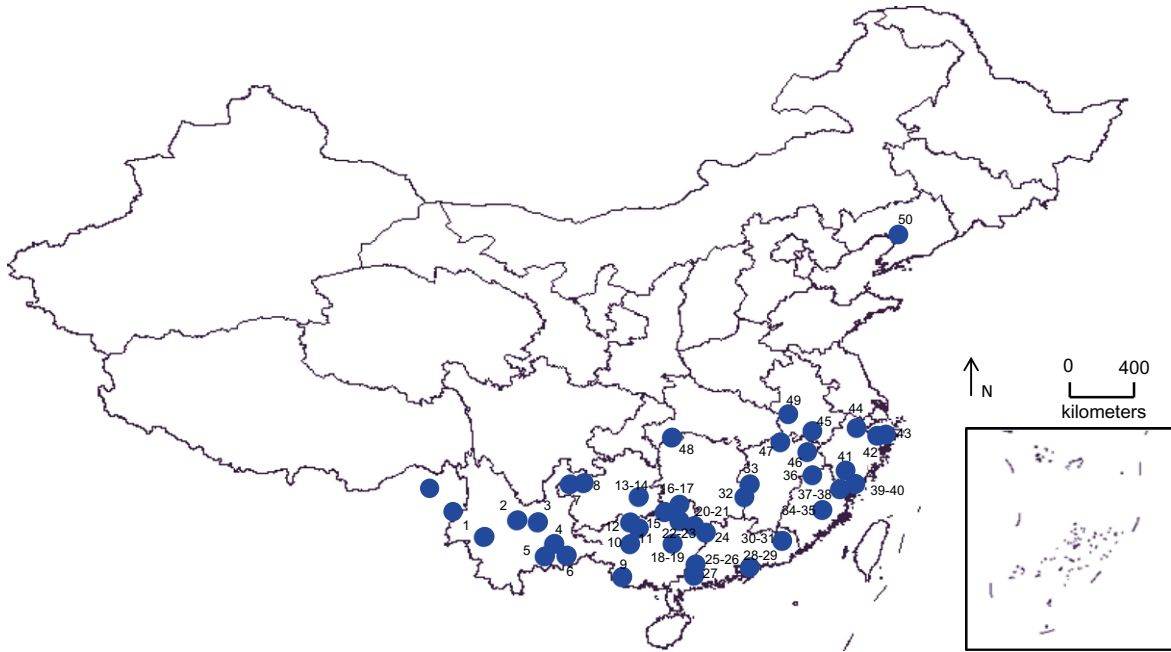
FIGURE 1 Sampling localities used in this study. Locality numbers refer to Table 1. The locality of *Echinotriton maxiquadratus* is not shown considering the potential illegal collection of this species

function of either water or air temperature. Again, we implemented the model in JAGS using the same settings.

3 | RESULTS

A total of 1,143 samples were collected from 36 Chinese salamander species from 51 localities (Table 1). All the newts appeared clinically healthy and no mortality events were detected. Bsal was found in 33 out of 1,143 samples (2.9%), including 3 of 4 species of *Cynops*, 1 of 7 species of *Pachytriton*, 2 of 11 species of *Paramesotriton*, 2 of 8 species of *Tylototriton*, and *A. davidianus* (Figure 2). In one population of *P. hongkongensis*, 65.6% of the sampled individuals were found to be infected, with the average true prevalence for this species estimated at 0.500 (95% CRI, 0.352, 0.648). The mean true prevalences at the level of individual species, genera, or provinces always fell within the range 0.01-0.06, with the exception of Guangdong Provence (mean 0.186, 95% CRI 0.125, 0.261) where high prevalence was largely determined by the above mentioned *P. hongkongensis* population (Figure 2). The true prevalence across all samples was estimated at 0.028 (95% CRI 0.020, 0.039). Sequencing of the amplicons yielded 100% similarity with that of the Bsal type strain (Martel et al., 2013). Bsal was found in salamanders occupying pools, streams, and land (Table 1). Bsal was detected in the range 4.5-24.9°C (air temperature) and 2.3-22.7°C (water temperature). We found Bsal prevalence to be negatively correlated to both air and water temperature across

our data set, but the effective variation was small and mostly reflected a scarcity of data at low temperatures; over the range 10-29°C (within which 95% of our air temperature samples were collected) the mean estimated true prevalence varied by less than 6% (Figure 3).

4 | DISCUSSION

We show Bsal to be present in wild populations of Chinese urodelans across a wide taxonomic, geographic, and environmental range. The overall low prevalence and low-grade infections support previous findings (Laking et al. 2017) of low-level endemism of Bsal in eastern Asia. Low prevalence of Bsal may explain why Zhu et al. (2014) failed to detect it in China, given the limited sample size in their study. At first glance, this overall low prevalence may suggest a low probability of entry in naïve regions such as the United States; indeed, our estimates are broadly consistent with the low levels of true prevalence (<1%) estimated for captive collections in the United States by Klocke et al. (2017), where Bsal was not detected. However, both the high prevalence in Hongkong newts (*P. hongkongensis*; which was not included in the survey by Klocke et al., 2017) and the mere presence in Chinese fire bellied newts (*C. orientalis*) are especially worrying, given the large-scale exploitation of these species for the international animal trade. Supposing a stable Bsal prevalence of 3% throughout the commercial chain, this would imply that at least an estimated 66,000 Bsal positive newts

TABLE 1 Screening of Chinese salamanders for the presence of Bsal

species	Locality	Habitat	Date (year/month/date)	Number Bsal positive/total number	Range of Bsal GE in positive samples	Air temperature (°C)	Water temperature (°C)
A. davidianus	Guangdong, Luodong, Nanchong farm 26	Stream	2017/06/14	1/16	4.612	22.3	19.5
Hynobius leechii	Liaoling, Anshan 50	Stream	2017/05/02	0/10	–	Not checked	Not checked
Cynops cyanurus	Yunnan, Chuxiong, Zixishan 2	Pool	2017/07/26	1/34	2.7	22.3	19.8
C. cyanurus	Yunnan, Kunming, Qipanshan 3	Pool	2017/07/27	1/26	5.7	20.1	17.5
Cynops fudingensis	Fujian, Fuding, Taimushan 39	Pool	2016/08/16	0/24	–	28.4	25.9
C. fudingensis	Fujian, Fuding, Jinfengsi 40	Pool	2017/06/19	0/47	–	24.3	22.1
Cynops glaucus	Guangdong, Peak of Tongguzhang 30	Pool	2016/08/17	0/26	–	26.7	23.8
C. glaucus	Guangdong, Tongguzhang, Kengwei 31	Pool	2017/06/17	0/3	–	19.7	16.2
C. orientalis	Jiangxi, Jiujiang, Guankoucun 47	Pool	2017/07/18	1/24	11.6	22.5	19.7
C. orientalis	Jiangxi, Pingle, Hongyancun 46	Pool	2017/07/20	0/53	–	27.1	24.7
C. orientalis	Zhejiang, Hangzhou 44	Pool	2017/04/19	0/18	–	25.3	23.1
Cynops orphicus	Fujian, Dehua, Lianhuachi 34	Pool	2017/06/23	1/16	2.22	17.8	15.9
Echinotriton chinhaiensis	Zhejiang, Ningbo, Yinzhou 42	Land	2016/08/15	0/2	–	29.3	No water
Echinotriton maxiquadratus	Guangdong 51	Land	2016/08/18	0/14	–	24.3	No water
Pachytriton archospotus	Jiangxi, Jinggangshan, Suangma 32	Stream	2017/06/30	0/49	–	22.3	19.6
Pachytriton brevipes	Fujian, Wuyishan, Guadun 36	Stream	2017/06/21	0/18	–	17.2	14.1
Pachytriton feii	Anhui, Qianxian, Hongxinxiang 45	Stream	2017/07/24	0/4	–	23.2	21.1
Pachytriton granulosus	Fujian, Dehua, Daiyunshan 35	Stream	2017/06/22	0/9	–	21.3	19.4
Pachytriton inexpectatus	Guizhou, Leishan, Leigongshan 14	Stream	2017/05/16	0/37	–	16.9	15.2
P. inexpectatus	Guangxi, Guilin, Maoershan, Gaozai 17	Stream	2017/07/11	0/15	–	23.5	21.6
P. inexpectatus	Guangxi, Laibin, Dayaoshan 18	Stream	2017/07/14	0/10	–	23.8	21.1
Pachytriton moi	Guangxi, Guilin, Maoershan, Antangpin 16	Stream	2017/07/08	0/14	–	23.5	21.6
P. moi	Guangxi, Guilin, Huaping 15	Stream	2017/07/12	0/36	–	24.2	21.8
Pachytriton wuguanfui	Guangxi, Hezhou,Sifang, Shishan 24	Stream	2017/06/25	1/25	2.9	24.9	22.7
Paramesotriton aurantius	Zhejiang, Zherong, Jiulongjin 37	Land	2016/08/16	0/5	–	27.1	No water
P. aurantius	Zhejiang, Lishui, Jingning, Jingnan 41	Stream	2017/02/08	2/30	4-484	4.5	2.3
P. aurantius	Fujian, Zherong, Longxi 38	Land	2017/06/19	2/21	1-10.2	18.6	No water
Paramesotriton caudopunctatus	Guizhou, Leishan, Leigongpin 13	Stream	2017/05/16	0/43	–	16.9	15.2
P. caudopunctatus	Guangxi, Hezhou, Gaozhai 22	Stream	2017/06/26	0/34	–	23.3	20.8

TABLE 1 Continued

species	Locality	Habitat	Date (year/month/date)	Number Bsal positive/total number	Range of Bsal GE in positive samples	Air temperature (°C)	Water temperature (°C)
P. caudopunctatus	Guangxi, Gongcheng, Sanlian 21	Stream	2017/06/27	0/5	–	21.7	19.2
Paramesotriton chinensis	Zhejiang, Ningbo, Baixi 43	Stream	2017/01/27	0/39	–	8.7	5.9
Paramesotriton deloustali	Yunnan, Honghe, Hekou 6	Stream	2017/04/05	0/13	–	24.2	21.7
Paramesotriton fuzhongensis	Guangxi, Hezhou, Gaoba 23	Stream	2017/06/26	0/11	–	23.3	20.8
P. fuzhongensis	Guangxi, Gongcheng, Huangpin 20	Stream	2017/06/27	0/42	–	21.7	19.2
Paramesotriton guanxiensis	Guangxi, Ningming, Nanan 9	Stream	2017/06/11	0/33	–	27.4	24.8
P. hongkongensis	Guangdong, Shenzheng, Yangmeiken 28	Stream	2016/08/20	0/10	–	31.2	28.6
P. hongkongensis	Guangdong, Shenzheng, Wutongshan 29	Stream	2017/02/14	21/32	10-84.6	17.3	15.1
Paramesotriton labiatus	Guangxi, Dayaoshan, Mengshanlu 19	Stream	2017/07/14	0/2	–	23.8	21.1
Paramesotriton qixilingensis	Jiangxi, Yongxin, Qixiling 33	Stream	2017/07/03	0/41	–	23.8	21.5
Paramesotriton yunwuensis	Guangdong, Luodong, Nanchong 25	Stream	2017/06/13	0/24	–	22.1	20.0
Paramesotriton zhijinensis	Guizhou, Bijie, Tianqingqiao 8	Stream	2017/05/14	0/22	–	17.6	15.1
Tylototriton asperrimus	Guangxi, Hechi, Qibainong 10	Pool	2017/05/20	0/16	–	17.4	15.7
T. asperrimus	Guangdong, Xinxuan, Dawuling 27	Pool	2017/07/15	1/7	16.1	20.0	18.2
Tylototriton broadoridgus	Hunan, Zhangjiajie, Badagongshan 48	Pool	2017/05/21	0/22	–	21.2	18.8
Tylototriton dabienicus	Anhui, Yaoluoping 49	Pool	2017/07/24	0/6	–	24.3	21.9
Tylototriton kweichowensis	Guizhou, Bijie, Gonglongping 7	Pool	2017/05/13	0/39	–	16.2	14.4
Tylototriton shanjing	Yunnan, Honghe, Huanglianshan 5	Pool	2017/06/05	0/16	–	24.8	22.3
Tylototriton verrucosus	Yunnan, Yongde, Daxueshan 1	Pool	2017/06/15	1/48	1.34	18.3	16
Tylototriton wenxianensis	Guangxi, Hechi, Chuanshan 11	Pool	2017/05/19	0/32	–	17.7	15.6
T. wenxianensis	Guizhou, Libo, Wengang 12	Pool	2017/05/18	0/10	–	19.9	17.1
Tylototriton yangi	Yunnan, Honghe, Gejiu 4	Pool	2017/05/10	0/9	–	19.6	17.2

The localities, habitats, sampling date, the total numbers of swabs and positive swabs for each locality, the range of Bsal GE in positive samples, air and water temperatures for each species in the wild are given.

"—" = no Bsal detection.

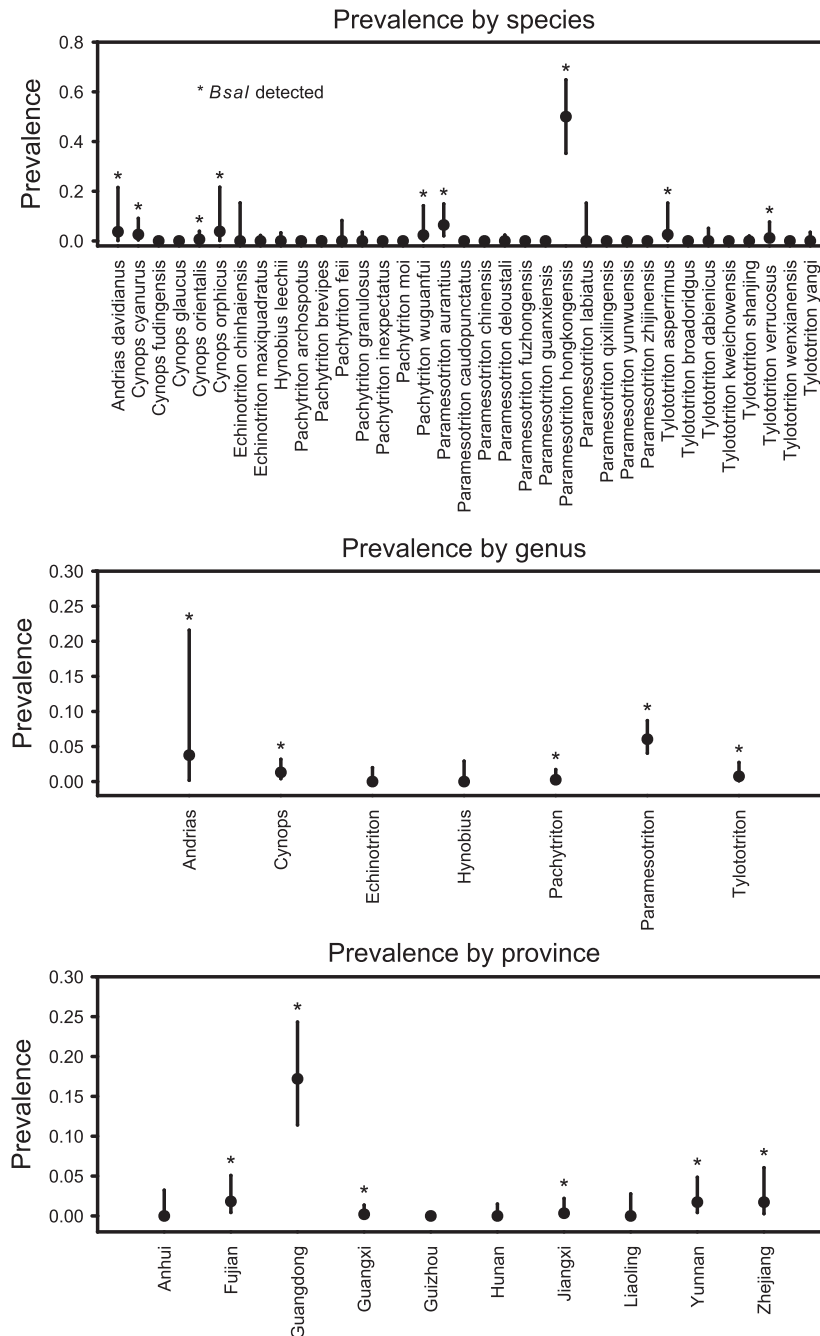The numbers followed the localities correspond to site numbers in Figure 1.

FIGURE 2 Estimated true prevalence of Bsal in Chinese urodelans. Bars indicate 95% CRI. Asterisks indicate species, genera, and provinces in which Bsal was detected

have reached the United States in the past decade. Once in captivity, Bsal has been demonstrated to jump from Asian to European species (Martel et al., 2014) and infect several non-Asian species (Cunningham et al., 2015; Sabino-Pinto et al., 2015), which increases opportunities for firm pathogen establishment and subsequent spillover to native amphibian communities through direct (intentional release or escape) or indirect transmission (e.g., double use of contaminated materials such as containers, dipnets for captive and wild urodelans). The recent identification of an environmentally resis-

tant life stage of Bsal (Stegen et al., 2017) further promotes transmission through environmental contamination (e.g., by waste water or discarded terrarium contents).

The presence of Bsal in urodelan species that are targeted for the pet trade support amphibian trade restrictions as currently in place in the United States, Canada, and Switzerland and emphasizes the urgent need for installing trade restrictions in Europe. Listing of Bsal by the World Organization for Animal Health in 2017 may further facilitate disease mitigation. Either trade bans or implementation of proper
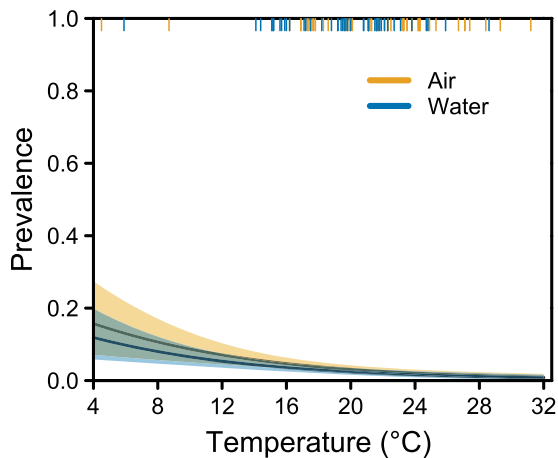
FIGURE 3 Correlation between estimated true prevalence of Bsal in Chinese urodelans and the air (orange) and water (blue) temperature recorded at the time and site of each sample collection. The shaded area indicates 95% CRI. The tick marks indicate the distribution of observed temperature data

sanitary measures (entry control, quarantine) could be effective. Our study provides prior information that is of vital importance to assess the requirements and effectiveness of biosecurity controls. The low prevalence of Bsal in asymptomatically infected Chinese urodeles (1-6% in the most heavily traded Chinese fire bellied newts) suggests that random sampling of a subset of imports may be insufficient to reliably detect Bsal in biosecurity controls. For example, even assuming a perfect test with 100% sensitivity were available, out of a batch of 100 salamanders, 79 should be tested to have a 99% chance of detecting Bsal if present at a prevalence of 0.03 (Cameron & Baldock, 1998). Ideally, every animal entering should be checked for the presence of Bsal.

Furthermore, reducing the risk of new Bsal entries may not suffice to avert the risk of further releases into naïve wild salamander populations, given its established presence in captive urodelan collections in Europe, which is likely mirrored in the United States. Eradicating Bsal from these captive collections is highly advisable and possible (Blooi et al., 2015; Sabino-Pinto et al., 2015), yet requires raising public awareness and building diagnostic capacity. Policy actions that involve all relevant stakeholders (including pet keepers) in a multistep preventive approach throughout the commercial chain are necessary to reduce the likelihood of introduction of Bsal in wild urodelan communities in naïve regions and prevent further loss of biodiversity.

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