

From dirty to delicacy? Changing exploitation in China threatens the world's largest amphibians

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Abstract

1. Determining the dynamics and sustainability of human interactions with threatened species is essential to inform evidence-based conservation, but data can be challenging to collect across large areas and multiple user groups.
2. Chinese giant salamanders *Andrias* spp. are critically depleted across China. Wild populations were exploited during the 20th century, and more recently to support a large-scale farming industry. However, robust data remain largely unavailable on the timing of population declines in relation to changing human pressures, on primary drivers of exploitation, or on the effectiveness of conservation legislation.
3. We conducted a series of large-scale interview surveys across the range of giant salamanders in China, targeting potential rural and urban user groups, and stakeholders involved with giant salamander exploitation and policy management (comprising 2,932 rural households, 66 salamander farms, 115 county government officials and 835 urban consumers).
4. Giant salamander populations were probably declining from at least the 1980s due to exploitation for food, and negative cultural values associated with these animals have not prevented rural consumption. There has been a major escalation in exploitation following the establishment of a large-scale giant salamander farming industry in the 2000s. Our results demonstrate wide-scale and largely unregulated illegal hunting to stock farms at a country-wide scale in order to support demand by urban consumers for high-prestige rare meat. We estimate there were at least 42,000 wild-caught breeding adult giant salamanders and 164,000 wild-caught subadults in farms across China at the time of our survey.
5. Salamander farming probably poses unsustainable pressure on giant salamander populations. Existing legislation has clearly proved ineffective at preventing the

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stocking of farms with wild-caught animals, and our findings highlight an important gap in the effectiveness of China's conservation protection for some of its highest-priority threatened species. Tackling this problem will likely require multiple coordinated approaches, including enforcement of legislation, increased penalties for removing giant salamanders from the wild, permanent identification of captive-bred giant salamanders, and consumer-focused interventions to reduce urban demand.

KEYWORDS

Andrias, Chinese giant salamander, cultural taboos, illegal wildlife trade, interview survey, overexploitation, traditional Chinese medicine, wildlife farming

1 | INTRODUCTION

Effective conservation of species that are threatened by exploitation requires a detailed understanding of human–wildlife interactions, including current patterns, levels and drivers of harmful behaviours by different user groups, the scales across which such interactions occur, and whether behaviour change over time has affected the sustainability of interactions (Nilsson et al., 2020; St John et al., 2013). Determining the dynamics and sustainability of human–wildlife interactions is of particular importance for conservation-priority species occurring within social-ecological systems in human-dominated landscapes, for example across eastern and southeast Asia, where threatened biodiversity coexists with high human population densities and is heavily exploited for local consumption and wider trade (Carter et al., 2012; Coggins, 2002; Liu et al., 2016; Zhang & Yin, 2014). Establishing robust baselines to inform evidence-based conservation for such systems is an interdisciplinary activity that typically requires the use of social science methods (Bennett et al., 2017; Lischka et al., 2018; Newing, 2010). However, such data can be challenging to collect systematically across large areas, or in an integrated manner for illegal activities or multiple key user groups, such as across supply chains from hunters to consumers (Challender & MacMillan, 2014).

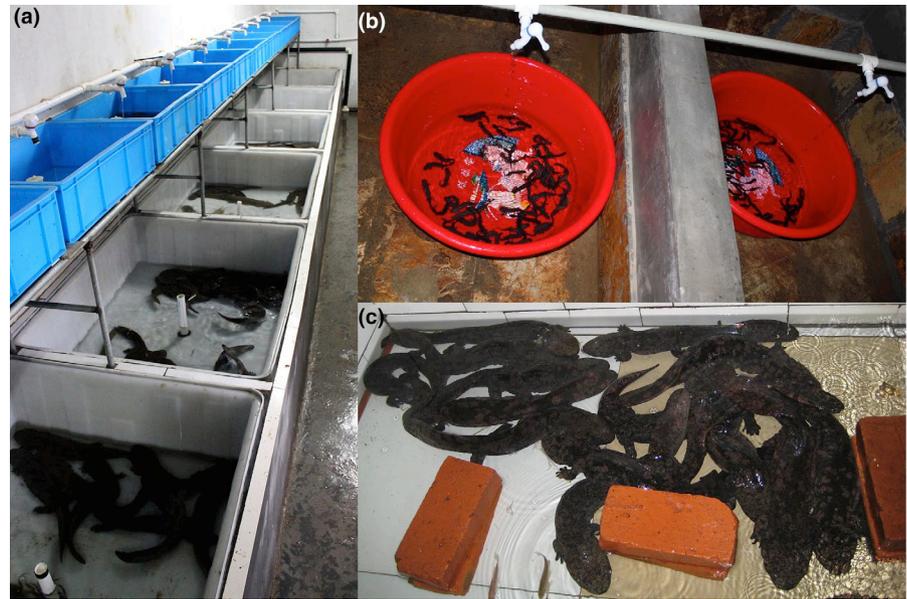
Chinese giant salamanders (Cryptobranchidae: *Andrias* spp.) are the world's largest amphibians, reaching almost 2 m in length and >50 kg in weight (Sowerby, 1925a, 1925b; Wang et al., 2004). They were historically distributed in fast-flowing montane rivers and streams across a large area of central, eastern and southern China, with records from 18 Chinese provinces or equivalent administrative regions (Chen et al., 2018; Fei et al., 2006; Huang, 1982; Wang et al., 2004). However, recent range-wide surveys have revealed that wild populations are now critically depleted or extirpated across China (Turvey et al., 2018). Allopatric populations have traditionally been interpreted as the single widely distributed species *Andrias davidianus*, which is assessed as Critically Endangered by IUCN (Liang et al., 2004), but recent genetic analysis has shown that they constitute a complex of at least three species, including the South China giant salamander *A. sligoi* and other undescribed taxa (Turvey et al., 2019; Yan et al., 2018).

Chinese giant salamanders are recognised as global conservation priorities on the basis of evolutionary history (Gumbs et al., 2018).

Anthropogenic modification of freshwater systems (e.g. pollutant emissions; alteration of flow regimes and water turbidity through damming) has reduced the availability of suitable giant salamander habitat (Dai et al., 2009; Wang et al., 2004). However, giant salamander populations have also been lost from unmodified habitats across China that still support diverse amphibian communities and abundant prey (Chen et al., 2018; Tapley et al., 2015, in press). Giant salamanders were designated as a State 2 Protected Animal in China in 1988, with this national legislation making hunting or collection illegal without an official permit (Dai et al., 2009). Despite their protected status, range-wide giant salamander declines have been attributed primarily to overexploitation (Tapley et al., in press).

The first western description of Chinese giant salamanders during the 19th century observed that 'such animals are a valuable alimentary resource for the inhabitants of the country' (Blanchard, 1871), and exploitation both for local consumption and for the domestic luxury food market occurred throughout the 20th century (Cunningham et al., 2016; Dai et al., 2009; Huang, 1982; Liu, 1950; Simoons, 1991; Sowerby, 1925a, 1925b; Wang et al., 2004). The use of giant salamanders in traditional Chinese medicine (TCM) has been documented for over 2000 years (Strassberg, 2002), with a wide range of perceived medicinal benefits (He et al., 2018). However, the extent to which these historical interactions impacted wild populations is unclear. It is also suggested that cultural taboos, associated with the concept that giant salamanders were 'dirty' or bad luck, may have limited the effects of exploitation until recently (Cunningham et al., 2016). A vast-scale giant salamander farming industry has developed rapidly in China since the 2000s (Figure 1). Whereas some level of captive breeding has been achieved by salamander farms, this industry has led to further pressure on wild populations to supply breeding stock, as well as posing risks of pathogen transfer, competition and hybridisation from farm releases or escapes (Cunningham et al., 2016; Turvey et al., 2018; Yan et al., 2018). Farms include large self-contained and privately owned facilities (company model); smaller-scale rearing of salamanders in individual

FIGURE 1 Typical company-model Chinese giant salamander farms. (a) Rearing pens for subadult giant salamanders (Shaanxi Province). Photograph courtesy of Benjamin Tapley/Zoological Society of London. (b) Rearing pens for giant salamander larvae (Guizhou Province). Photograph courtesy of Benjamin Tapley/Zoological Society of London. (c) Close-up of rearing pen for subadult giant salamanders, showing high stocking density (Shaanxi Province). Photograph courtesy of Minyao Wu



households, often in association with company-model farms (small-holder model); and breeding co-operatives, often with a centralised facility (Cunningham et al., 2016).

Understanding the causes and impacts of these various pressures on wild populations, identifying which specific demands and user-groups are the greatest drivers of exploitation, and assessing the effectiveness of existing legislation and conservation management, are all necessary before appropriate mitigations can be developed to combat further giant salamander declines. However, numerous crucial aspects of giant salamander exploitation remain unclear, including whether population declines are recent or pre-date the farming industry; levels of stocking of wild-caught versus farm-bred individuals in farms, and the legality of exploitation of wild populations to stock farms; and what factors drive and regulate consumer demand, including the relative importance of consumption for food versus medicinal use, whether any cultural restrictions limit consumption, and why giant salamanders are considered desirable to eat in China. There is an urgent need for improved baselines to understand the dynamics and drivers of giant salamander decline, and the sustainability or otherwise of past and present interactions with wild populations.

In order to strengthen the scientific evidence-base on past and present activities associated with giant salamander declines, we conducted a series of large-scale social science surveys across the range of giant salamanders in China, targeting multiple potential user groups in both rural and urban contexts, and stakeholders directly involved with both giant salamander exploitation and policy management. Our results provide crucial information on the sustainability of human–salamander interactions over time, drivers of demand, and the effectiveness of existing conservation policy. We establish an important new baseline to guide future conservation decision-making, and a wider template for investigating human–wildlife interactions operating across large scales and complex social-ecological systems.

2 | MATERIAL AND METHODS

Between May 2013 and June 2016, we conducted interviews with four different respondent groups in China: rural households living in close proximity to potential giant salamander habitat; company members in company-model salamander farms; county-level government fishery bureau officials; and urban respondents representing potential end-consumers (Table 1). Different standard questionnaires containing multiple open-ended questions were used for each respondent group (Text S1). All interviews were conducted in Chinese (either standard Mandarin or a local dialect) by the authors and Chinese field teams comprising staff and students from local academic institutions, who received training in standardised interview techniques before fieldwork commenced. We explained that we were conducting interviews to research knowledge of local wildlife and aquatic resources, obtained informed verbal consent before all interviews, and informed respondents they could stop at any time. Verbal rather than written consent was obtained because many respondents had low levels of literacy, and/or were cautious about signing documents. Rural and urban questionnaires were anonymous; names and positions of farm company members and government officials were initially recorded to allow future follow-up if necessary, but were not recorded in final datasheets. Project design was approved by the Zoological Society of London's ethics committee (ref. WLE569), and by Chinese government authorities in all provinces where fieldwork was conducted.

Rural household surveys were conducted in 99 counties across 16 provinces or equivalent administrative regions. We randomly selected respondents by traversing villages on foot, and gathered interview data on respondents' demographic characteristics, traditional knowledge and attitudes regarding giant salamanders, and patterns of local usage including consumption for food and use in TCM. All counties had historical records of giant salamanders and/or >50%

TABLE 1 Summary of respondent samples for interview surveys conducted in China in 2013–2016

Survey	Respondents	Sample size	Counties/cities	Provinces
Rural household survey	Households close to giant salamander habitat; potential sources of traditional knowledge and experience of local exploitation/usage	2,932	99	16
Farm survey	Company members in company-model giant salamander farms	66	62	12
County survey	County-level government fishery bureau officials	115	115	10
Urban consumer survey	Potential urban end-consumers	835	3	3

predicted suitable giant salamander habitat based on the habitat suitability model of Chen et al. (2018). All communities were situated within 1 km of intact natural habitat (fast-flowing mountain streams with riparian forest cover and rocky substrates), determined through discussion with local government fisheries or forestry bureau officials. Full details of rural interview methods are given in Tapley et al. (2017), Chen et al. (2018) and Turvey et al. (2018).

Interviews with farm company members and government officials were mainly conducted in person, with some county-level fisheries staff contacted via email by province-level or municipality-level fisheries staff (i.e. staff at higher administrative levels) on our behalf. Farms were identified through discussion with fisheries staff. Farm interviews gathered data on the history of the farm, stock composition and origin, and stocking preferences. Government interviews gathered data on local legislation and enforcement including reports of illegal poaching or trading, permits to collect wild salamanders, and numbers of licensed farms under their jurisdiction. Interviews with members of the general public living in urban centres were conducted in three provincial capital cities (Guiyang, Kunming, Xi'an), with respondents selected through random encounters for face-to-face interviews in parks, museums and residential districts. Urban interviews gathered data on demographic characteristics of respondents; whether they knew of anyone who had eaten giant salamander (to establish levels of urban salamander consumption across respondents' wider social networks and beyond their direct personal experience, e.g. if salamanders are preferentially consumed only at high-status banquets); and reasons why they might want to eat giant salamander. Additional data also collected during interviews have been analysed and reported elsewhere (Chen et al., 2018; Turvey et al., 2018; Tapley et al., in press).

Salamander last-consumption dates were reported in a variety of formats (e.g. years ago; decadal ranges), and were converted to direct calendar years for analysis. Responses of 'when I was small' or 'when I was a child' were randomly assigned a date within the year range when the respondent was between 8 and 15 years old, and we converted all other records following Turvey, Bryant, et al. (2017) unless reported dates were too vague to include in analysis.

We constructed multivariate additive generalised linear models (GLMs) to investigate factors predicting the likelihood that: (a) rural respondents had eaten giant salamander; (b) urban respondents knew someone who had eaten giant salamander; and (c) urban respondents wanted to eat giant salamander because of specific reasons reported in >5% of interviews. All GLMs had binary responses

('yes'/'no'), binomial error structure and logit link function. GLMs investigating factors associated with rural respondents having eaten salamanders included respondent age, gender, ethnicity and province as fixed effects, and were conducted using two model structures: (a) including ethnicity as a binary variable (Han vs. non-Han ethnic groups); (b) including all ethnic groups represented in our dataset by ≥ 10 respondents as separate categories ($n = 11$). GLMs investigating urban respondent responses included respondent age, gender, education level and city as fixed effects. We also used a chi-square test to investigate whether rural respondents who reported that giant salamanders were 'unlucky' or 'bad luck' showed a different likelihood of reporting having eaten them. We analysed all data using R version 3.2.3 (R Development Core Team, 2015).

3 | RESULTS

3.1 | Rural household survey

We interviewed 2,932 respondents (mean age, 47.3; age range, 18–89; male, 69.9%; female, 30.1%; Table S1). The majority of respondents were of Han ethnicity (70.4%), but our total respondent sample also included 16 other ethnic groups (Bai, Buyi, Dong, Gelao, Hui, Lian, Miao, Panyao, Qijia, She, Tong, Tujia, Yao, Yi, Zang, Zhuang). The majority of respondents were rural subsistence farmers (86.4%). Not all respondents answered all questions.

In total, 83.9% of respondents could recognise giant salamanders. Local names (27 names or variants) were reported by 593 respondents (20.2%). The commonest reported local names (named by >20 respondents) were: (a) 'dog-fish' (*gouyu*), $n = 220$ (Guangxi, Guizhou, Hunan, Jiangxi), and the related names 'cured dog-meat' or 'dog-sausage' (*lagou*), $n = 38$ (Hunan) and 'puppy-fish' (*gouzaiyu*), $n = 3$ (Guangxi); (b) 'baby-fish' (*wawayu*), $n = 194$ (Anhui, Guangxi, Henan, Hubei, Hunan, Jiangxi, Yunnan, Zhejiang); (c) 'four-legged fish' (*sijiaoyu*), $n = 86$ (Anhui, Zhejiang); (d) 'old rock fish' (*laoyanyu*), $n = 22$ (Guizhou).

Local traditions, legends or stories about salamanders were reported by 106 respondents from 12 provinces (Anhui, Chongqing, Fujian, Gansu, Henan, Hubei, Hunan, Jiangxi, Shaanxi, Sichuan, Yunnan, Zhejiang); nearly all respondents were of Han ethnicity, except for two Tujia respondents and single Miao, She and Yi respondents. Traditions fell into two major categories: (a) connection to children ($n = 66$), including: supposed similarity in crying sound

($n = 29$) or appearance ($n = 4$); babies turn into salamanders ($n = 32$), including specifically illegitimate babies ($n = 4$) or dead babies ($n = 15$); salamanders eat children ($n = 5$), usually dead children or corpses in general ($n = 4$); (b) bad luck, or forbidden/taboo to eat them ($n = 37$), sometimes specifically because they had transformed from dead babies ($n = 10$).

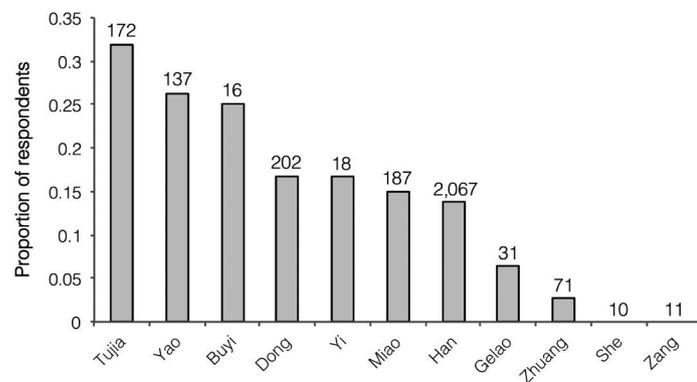
In total, 234 respondents (8.0%) reported that salamanders could be used for TCM, and 203 respondents reported specific uses. These were most frequently associated with healing or modifying skin (often specifically using salamander skin or mucus), including treating burns ($n = 118$), skin diseases such as leprosy ($n = 9$) or wounds/cuts ($n = 4$), and improving one's looks ($n = 14$). However, only 15 respondents from six provinces (0.5%) reported ever having used salamanders for medicinal purposes, and only one person (from Shaanxi) had used them since 2000.

Only 206 respondents (7.0%) reported having ever caught a giant salamander. However, 452 respondents (15.4%) reported having eaten giant salamander. Province, age and gender were highly significant in both GLMs, with men and older people more likely to

report having eaten giant salamander (*male gender*: binary model, $est = 0.563$, $SE = 0.133$, $z\text{-value} = 4.235$, $p < 0.0001$; *non-binary gender*: binary model, $est = 0.652$, $SE = 0.136$, $z\text{-value} = 4.781$, $p < 0.0001$; *age*: binary model, $est = 0.043$, $SE = 0.004$, $z\text{-value} = 10.277$, $p < 0.0001$; *non-binary age*: binary model, $est = 0.042$, $SE = 0.004$, $z\text{-value} = 9.950$, $p < 0.0001$; see Table S2 for full results; Figures 2 and 3a). In the binary ethnic model ($n = 2,929$ respondents), non-Han respondents (168/864, 19.4%) were more likely to report having eaten giant salamander compared to Han respondents (283/2,065, 13.7%; $est = 0.453$, $SE = 0.135$, $z\text{-value} = 3.353$, $p = 0.0008$). In the non-binary, multi-ethnic model ($n = 2,921$ respondents), Tujia respondents (Chongqing, Guizhou, Hubei, Hunan; 55/172, 32.0%) and Yao respondents (Guangdong, Guangxi, Hunan; 36/137, 26.3%) were more likely to report having eaten giant salamander compared to Han respondents (*Tujia*: $est = 1.402$, $SE = 0.235$, $z\text{-value} = 5.976$, $p < 0.0001$; *Yao*: $est = 0.895$, $SE = 0.295$, $z\text{-value} = 3.032$, $p = 0.002$), and Zhuang respondents (Guangxi; 2/71, 2.8%) were less likely to report having eaten giant salamander compared to Han respondents ($est = -1.723$, $SE = 0.758$, $z\text{-value} = -2.274$,



FIGURE 2 (Top) Proportions of respondents from rural households who reported having eaten giant salamanders in each of 16 surveyed provinces. Numbers within pie charts indicate number of respondents interviewed in each province. (Bottom) Proportions of respondents from rural households who reported having eaten giant salamanders, across Chinese ethnic groups represented by ≥ 10 respondents in our survey. Numbers indicate number of respondents interviewed for each ethnic group



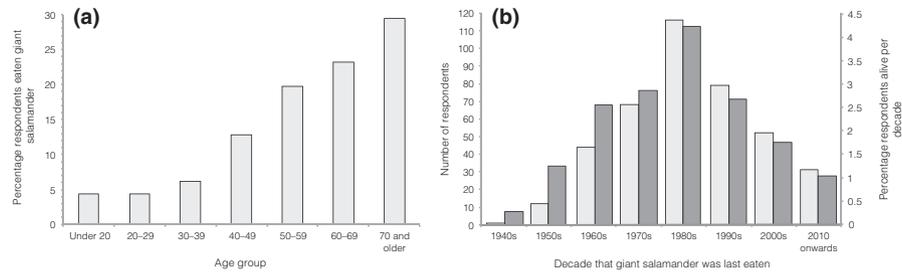


FIGURE 3 (a) Percentage of respondents of different age classes from rural households who reported having eaten giant salamanders. (b) Decade that respondents from rural households reported having last eaten giant salamander. *Pale grey*, number of respondents reporting last consumption dates in each decade; *dark grey*, percentage of respondents reporting last consumption dates per decade relative to total number of respondents alive in that decade

$p = 0.023$; Figure 2). For the subset of respondents from provinces where local traditions of bad luck associated with salamanders were reported (Anhui, Chongqing, Hubei, Shaanxi, Sichuan, Yunnan; $n = 779$), people who reported that giant salamanders were ‘unlucky’ or ‘bad luck’ were more likely to have eaten them (*bad luck*: 23/37 eaten, 62.2%; *not bad luck*: 137/742 eaten, 18.5%; $\chi^2 = 38.601$, $df = 1$, $p < 0.0001$).

Giant salamander last-consumption dates were reported by 403 respondents. Dates ranged from the 1940s to the 2010s. When grouped into decadal bins, only 20.6% (83/403) of these respondents had eaten giant salamander from 2000 onwards, and the highest proportion had not eaten them since the 1980s (28.8%, 116/403). To control for the fact that fewer respondents will have been alive (and thus able to eat salamanders) longer ago, data were recalculated relative to the total number of respondents who were alive in each decade, and retain a highest last consumption peak in the 1980s (Figure 3b).

3.2 | Farm survey

We collected data from 66 farms in 62 counties across 12 provinces (Chongqing, $n = 6$; Fujian, $n = 1$; Gansu, $n = 1$; Guangdong, $n = 1$; Guangxi, $n = 7$; Guizhou, $n = 19$; Henan, $n = 1$; Hubei, $n = 4$; Hunan, $n = 13$; Shaanxi, $n = 2$; Sichuan, $n = 10$; Yunnan, $n = 1$; Table S3). Mean number of years since farm establishment was 5.9 (range, 0–21 years). Twenty-five farms (37.9%) in nine provinces (Chongqing, Fujian, Guangxi, Guizhou, Henan, Hubei, Shaanxi, Sichuan, Yunnan) reported their stock included wild-caught salamanders: breeding adults, 24 farms, mean = 43.8 individuals, range = 2–300 individuals; subadults, nine farms, mean = 459 individuals, range = 2–3000 individuals; larvae, four farms, mean = 144 individuals, range = 10–250 individuals. Of these farms, 22/25 (88%) reported that wild-caught salamanders were all obtained locally; two farms reported that all wild-caught animals (including adults, subadults and larvae) were from a different county or neighbouring province, and one farm reported that it contained adults that were both locally caught and from a neighbouring province. In total, 49 farms (74.2%) reported that wild salamanders occurred in the area, and 39 farms (59.1%) provided

details of specific localities or regions where they knew wild salamanders could be caught.

Forty farms (60.6%) reported a preference for stocking with either wild or farmed salamanders, with 31 (47.0%) preferring wild stock and nine (13.6%) preferring farmed stock. Reasons given for preferring wild stock included: use in propagation, for example better reproductive output and/or growth rates ($n = 16$); better viability and disease resistance ($n = 8$); better ‘adaptability’ ($n = 3$); better taste/more nutritious ($n = 2$). Reasons given for preferring farmed stock included: cheaper ($n = 3$); more docile/easier to look after ($n = 3$); better survival rate ($n = 1$); can use hormones to enhance reproduction ($n = 1$).

3.3 | County survey

We collected data from county-level officials in 115 counties across 10 provinces (Chongqing, $n = 6$; Fujian, $n = 1$; Guangdong, $n = 1$; Guangxi, $n = 9$; Guizhou, $n = 27$; Henan, $n = 8$; Hubei, $n = 24$; Hunan, $n = 13$; Sichuan, $n = 22$; Zhejiang, $n = 4$; Table S4). Of these counties, 27 (23.5%) provided reports of illegal salamander poaching or trading, which led to penalties (fines) in 18 counties (15.7%); dates were provided for 17 reports, with 10 dating from the 1990s (i.e. before the farming industry had developed), and only seven dating from the past decade. Officials in only seven counties (5.9%) had issued permits to allow collection of wild salamanders.

Salamander farms were reported from 84 counties by officials (73.0%), including company-model farms in 52 counties (45.2%; mean of 3.31/county for these counties; range, 1–15), collaborative-model farms in 32 counties (27.8%; mean of 4.69/county for these counties; range, 1–40), and household-model farms in 51 counties (44.3%; mean of 131.5/county for these counties; range, 1–2,000). Data for farm and county surveys had 44 counties in common. Farms in 12 of these counties (in Guangxi, Guizhou, Henan, Hubei and Sichuan) reported containing locally wild-caught salamanders. Of these 12 counties, officials in only one (Xingwen County, Sichuan) had issued permits to collect wild salamanders, but officials in four counties provided reports of illegal salamander poaching or trading, with fines given for illegal poaching in one county.

3.4 | Urban consumer survey

We interviewed 835 respondents who answered all questions on knowledge and attitudes about giant salamander consumption (male, 42.9%; female, 57.1%; Table S5). Of these respondents, 273 (32.7%) knew someone who had eaten giant salamander (Guiyang, 44.5%; Kunming, 28.3%; Xi'an, 26.8%). Older age, male gender, higher education level and living in Guiyang were all associated with increased likelihood of knowing someone who had eaten giant salamander (*age*: $est = 0.265$, $SE = 0.079$, $z\text{-value} = 3.370$, $p = 0.0008$; *male gender*: $est = 0.398$, $SE = 0.153$, $z\text{-value} = 2.603$, $p = 0.009$; *education level*: $est = 0.391$, $SE = 0.118$, $z\text{-value} = 3.307$, $p = 0.0009$; *living in Kunming*: $est = -1.021$, $SE = 0.205$, $z\text{-value} = -4.968$, $p < 0.0001$; *living in Xi'an*: $est = -0.938$, $SE = 0.195$, $z\text{-value} = -4.822$, $p < 0.0001$).

The commonest reasons given for eating giant salamander included rarity or expensiveness ($n = 138$, 16.5%), curiosity ($n = 111$, 13.3%), good flavour ($n = 80$, 9.6%), and health benefits due to lack of pollution ($n = 20$, 2.4%). No demographic or geographic predictors were statistically correlated in GLMs with wanting to eat giant salamander due to rarity/expensiveness or respondent curiosity (all $p > 0.05$); increased likelihood of wanting to eat giant salamander because of perceived good flavour was associated with older age, male gender and living in Guiyang (*age*: $est = 0.257$, $SE = 0.119$, $z\text{-value} = 2.162$, $p = 0.031$; *male gender*: $est = 0.520$, $SE = 0.242$, $z\text{-value} = 2.149$, $p = 0.032$; *living in Kunming*: $est = -0.928$, $SE = 0.308$, $z\text{-value} = -3.008$, $p = 0.003$; *living in Xi'an*: $est = -0.992$, $SE = 0.305$, $z\text{-value} = -3.250$, $p = 0.001$).

4 | DISCUSSION

We collected and analysed multiple large-scale social science datasets, based on interviews with 3,948 respondents across China representing all key stakeholder groups from hunters to end-consumers, to understand the likely sustainability of past and present exploitation of wild giant salamander populations. This integrated approach provides important new insights about the dynamics and drivers of human-wildlife interactions across the giant salamander exploitation chain in China, as well as the effectiveness of existing regulations that aim to protect wild populations of these Critically Endangered species.

Our rural household survey sampled a wide range of local traditions and indigenous knowledge associated with different ethnic cultures across the extensive distribution of giant salamanders in China, as demonstrated by the diversity of reported local names for these animals. Interestingly, whereas the colloquial name *wawayu* or 'baby-fish' (supposedly so-called because giant salamanders sound like crying babies) is said to be common across China (Dai et al., 2009; Huang, 1982; Wang et al., 2004), this name was reported by a relatively small subset of respondents, and was often linked to a perceived association with dead babies rather than baby-like vocalisations. Older historical accounts also refer to differing local names (Liu, 1950; Strassberg, 2002). Our results also reveal complex patterns of rural consumption of giant salamanders across China,

with variation associated with both geography and different ethnic groups. These findings indicate that region-specific and/or Han-based narratives of limited past local consumption of giant salamanders, such as provided by informants in Cunningham et al. (2016), may not be widely representative, and provide further evidence that different cultures across China have very different patterns of sustainable or unsustainable interaction with local environments and natural resources (Jiao et al., 2012; Zhang et al., 2020). Nuanced region-specific management policies may therefore be necessary to regulate local rural interactions with giant salamander populations effectively. However, extensive consumption is documented across the likely distributions of all recently recognised Chinese giant salamander species (Turvey et al., 2019; Yan et al., 2018).

Overexploitation for TCM poses a major threat to many threatened species, both within China and through international trade (Chen et al., 2015; Cheng et al., 2017; O'Malley et al., 2017; Wong, 2019). Rural respondents were aware of multiple medicinal uses for giant salamanders, which are similar to advertised uses for giant salamanders in modern-day commercial TCM (He et al., 2018). Overall, however, very few people in these communities have ever actually used these animals for medicinal purposes, indicating that such usage was probably never a major threat to wild populations. Conversely, a substantial number of rural respondents reported having eaten giant salamanders, and this reported level might represent an underestimate due to the potential sensitivity of this activity. Our results indicate that consumption of giant salamanders in rural communities was more common in the past, with about a quarter of older respondents having formerly eaten them in contrast to much lower numbers of younger respondents, and with a marked drop-off in consumption since the 1980s.

It is difficult to reconstruct population declines retrospectively in the absence of contemporary longitudinal monitoring data, and this shift in giant salamander consumption might reflect cultural or economic changes in China during recent history. For example, low-income rural communities may have been more dependent upon wild protein sources before implementation of free-market reforms that prompted nation-wide economic growth from the 1980s onwards. Indeed, respondents from both Shaanxi and Sichuan reported that giant salamanders were low-class meat, with another respondent from Sichuan reporting that giant salamander meat cost 0.6 yuan per kg in the 1970s and was far cheaper than pork. However, the mid-late 20th century is regarded as a period of largely uncontrolled wildlife exploitation in China, suggesting that giant salamanders are also likely to have been overexploited during this period (Corlett, 2007; Lau et al., 2010; Turvey, Crees, et al., 2017). Our results thus provide indirect evidence that giant salamander populations in areas of good-quality habitat were probably already declining from at least the 1980s, due to local consumption and/or exploitation for trade, and several decades before the development of the modern farming industry.

Our results confirm that giant salamanders were considered 'dirty' and associated with bad luck in rural communities across many parts of China, usually due to a perceived association with dead

children, and with species-specific cultural taboos reported against eating them by several respondents. Interestingly, some other 'liminal' animals are also associated with dead children (e.g. nightjars in historical English tradition; Greenoak, 1997). Comparable taboos are widespread across other social-ecological systems, and can play important conservation roles by influencing societal preferences and supporting sustainable behaviours at local scales (Colding & Folke, 2001; Jones et al., 2008; Lingard et al., 2003). However, our results also demonstrate that reported taboos against eating giant salamanders have apparently not been effective during recent history; the negative cultural values associated with these animals have not prevented local people from eating them, and respondent knowledge of such taboos is actually associated with a higher likelihood of past consumption. Although patterns and drivers of taboo stability or erosion are complex, increasing non-adherence to existing wildlife consumption taboos has been associated with rapid social change in other systems, as has taken place in China throughout recent decades (Golden & Comaroff, 2015). Our study therefore provides new evidence that local taboos are not always effective at limiting exploitation of target species, possibly because changing socio-cultural pressures may have weakened this form of traditional management, and these cultural traditions are therefore unlikely to be of use for reducing local pressures on giant salamander populations.

Whereas rural communities now rarely consume giant salamanders, our data show that a large proportion of recently established farms across China admit to stocking wild-caught animals, that many farmers know where to locate wild salamanders to stock farms, and farms often have a specific preference for wild rather than farm-bred stock. Indeed, we interpret our figures as likely underestimates, as farms might not admit to possessing wild-caught individuals due to the potentially sensitive nature of obtaining this stock. These findings therefore provide compelling evidence for a major escalation in direct exploitation of wild populations since the establishment of the giant salamander farming industry. Comparison of data from our farm and county surveys also indicates that the great majority of wild-caught salamanders in farms must have been obtained illegally, since many farms report possessing locally wild-caught stock but almost no government permits have been issued for collection in these counties, whereas fines have been issued for illegal poaching of giant salamanders. Whilst some of these wild-caught animals might represent confiscated stock that have been transferred to farms (Cunningham et al., 2016), most farms with locally wild-caught giant salamanders thus appear to have obtained their stock illegally, and existing protective legislation has clearly proved ineffective at preventing wide-scale stocking of farms with wild-caught animals. This scenario shows striking parallels to turtle farming in China. Freshwater turtles are widely consumed in China and used in TCM (van Dijk, 2000), and Chinese turtle farms are known to launder wild-caught animals and are significant purchasers of wild turtles (Gaillard et al., 2017; Shi et al., 2007, 2008). Comparable patterns of illegal acquisition of wild-caught stock to supply commercial farms are also seen across other exploited wildlife species in eastern and southeast Asia, such as in farming of porcupines *Hystrix brachyura* in Vietnam (Brooks et al., 2010).

There were 2,622 company-model salamander farms, of which 2,080 were legally licensed, across China at the end of 2013 (Li, 2015). Using this figure to extrapolate from the results of our farm survey (which sampled 62 counties across 12 provinces from 2013 onwards and is thus representative of contemporary nation-wide farming patterns), we estimate there may have been approximately 42,000 wild-caught breeding adult giant salamanders and 164,000 wild-caught subadults in company-model farms across China at this time. This estimate does not account for additional wild-caught animals also likely to be held across China in smallholder-model farms and breeding co-operatives. Although we have no information on the rate of turnover of wild-caught farm stock (e.g. movement between farms or trade to restaurants, death due to disease) and/or the rate of extraction of wild animals to supply farms in relation to this turnover, our estimate clearly demonstrates that the recently developed farming industry poses tremendous pressure on remaining populations of giant salamanders across China. No estimates of historical (pre-exploitation) population size are available for Chinese giant salamander species, and the size and distribution of surviving depleted populations is also uncertain (Turvey et al., 2018). However, we consider that this level of extraction of wild individuals is probably unsustainable for a long-lived, slow-reproducing apex predator (cf. Cheng, 1998; Huang, 1982).

Finally, our urban interviews reveal that consumption of giant salamanders in Chinese cities is relatively widespread, and shows a positive correlation with respondent education level that is likely associated with the luxury status of this commodity. Respondents in Guiyang, the smallest and least developed of the Chinese urban centres we surveyed, were more likely than respondents in Kunming or Xi'an to know someone who had eaten giant salamander and to want to eat giant salamander because of perceived good flavour. This might reflect the high habitat suitability and likely former abundance of giant salamanders in Guizhou Province (Chen et al., 2018), and their documented local trade for food in Guiyang before the recent establishment of the salamander farming industry, suggesting a possible long local tradition of consumption (Sowerby, 1925a, 1925b); however, over a quarter of respondents in Kunming or Xi'an also knew people who had eaten giant salamanders. Concerningly, the most commonly reported reason by urban respondents for wanting to eat a giant salamander was the animal's rarity or expensiveness. Other threatened species also constitute luxury foods in China, and rare meat types are often preferentially consumed as indicators of wealth and status in Asian cultures (Fabinyi, 2011; Fabinyi & Liu, 2014; Shairp et al., 2016); however, placing value on rarity can drive disproportionate exploitation of rare species, potentially leading to an extinction vortex (Courchamp et al., 2006). Whereas both demographic and geographic variables are associated with respondent knowledge of giant salamander consumption, the desire to eat salamanders due to either rarity or curiosity was not correlated with any of our variables. Our results thus suggest that this driver of demand for giant salamanders may be widespread across the potential urban consumer market in China, making it difficult to reduce such demand through educational targeting or other interventions

aimed at specific user groups. Once again, these findings are similar to freshwater turtle trade and consumption dynamics in China, where wild turtle meat commands a higher price than farmed turtle meat (Gaillard et al., 2017; Shi et al., 2007).

Our comprehensive assessment of patterns, levels and drivers of interactions with giant salamanders by multiple user-groups across China establishes an important new baseline for assessing the impacts of past and present exploitation, and our findings raise worrying concerns for the future of wild populations of these remarkable animals. It is likely that giant salamander populations were already in decline several decades ago as a result of historical exploitation; and such exploitation has clearly intensified recently due to largely unregulated illegal hunting to stock and maintain large wild-caught salamander populations in farms at a country-wide scale to support demand by urban consumers for high-prestige rare meat. These findings highlight an important and concerning gap in the effectiveness of China's existing conservation protection for some of its highest-priority threatened species; they will be used to inform updated extinction risk assessments and national conservation action planning for Chinese giant salamander species, and to develop regional and national management interventions that involve both government and civil society. Tackling this problem will likely require multiple coordinated approaches, including further research into sustainable salamander offtake levels and how to counter consumer preference for rare species, strengthened enforcement of existing legislation to prevent ongoing poaching, increased penalties for removing giant salamanders from the wild, and the permanent identification of captive-bred giant salamanders. Existing wild-caught farm stocks could be used to establish separately managed species-specific conservation breeding programmes should wild founding stock be unavailable (Cunningham et al., 2016; Turvey et al., 2018). We also recommend consumer-focused interventions to reduce urban demand, for example by encouraging socially responsible consumption (Yan & She, 2011).

Our research was conducted after Chinese president Xi Jinping initiated an ongoing nation-wide anti-corruption campaign in 2012, which targeted consumption of high-prestige rare animal products at official banquets; the high level of exploitation of giant salamanders demonstrated in our study is thus from the period when demand for consumption at banquets had likely already declined. We note that the COVID-19 pandemic has led to further restrictions on trade in rare and luxury wild animal products in China. Although these restrictions do not apply specifically to giant salamanders, we hope that the new regulations will benefit giant salamander conservation by reducing wider exploitation, demand and perceptions of wild meat. However, additional targeted and proactive interventions are now imperative to reduce the ongoing pressure on wild populations of giant salamanders across China, in order to save these unique 'living fossils'.

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CONFLICT OF INTEREST

The authors report no conflict of interest.

AUTHORS' CONTRIBUTIONS

S.T.T., A.A.C., S.C. and B.T. designed research; S.C., A.A.C. and S.T.T. coordinated data collection, and all authors collected data; S.T.T. interpreted and analysed data, and wrote the paper with assistance from A.A.C. and B.T.

DATA AVAILABILITY STATEMENT

The datasets supporting this paper (interview data for different respondent groups in China) are available in the electronic supplementary material, and are also available online at University College London's Research Data Repository: <https://doi.org/10.5522/04/13469022.v1> (Turvey et al., 2021a), <https://doi.org/10.5522/04/13469085.v1> (Turvey et al., 2021b), <https://doi.org/10.5522/04/13469139.v1> (Turvey et al., 2021c), <https://doi.org/10.5522/04/13469166.v1> (Turvey et al., 2021d).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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