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Spatial and temporal extinction dynamics in a freshwater cetacean

Samuel T. Turvey[1,*], Leigh A. Barrett[2], Tom Hart[1], Ben Collen[1], Hao Yujiang[3,*], Zhang Lei[3], Zhang Xinqiao[3], Wang Xianyan[3], Huang Yadong[3], Zhou Kaiya[4] and Wang Ding[3]

[1]*Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK*
[2]*vaquita.org Foundation, 6048 Dassia Way, Oceanside, CA 92056, USA*
[3]*Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, People's Republic of China*
[4]*Jiangsu Key Laboratory for Biodiversity and Biotechnology, College of Life Sciences, Nanjing Normal University, Nanjing 210097, People's Republic of China*

Geographical range contraction is a fundamental ecological characteristic of species population decline, but relatively little investigation has been conducted into general trends in the dynamic properties of range collapse. The Yangtze River dolphin or baiji (*Lipotes vexillifer*), probably the first large mammal species to have become extinct in over 50 years, was believed to have experienced major range collapse during its decline through progressive large-scale range contraction and fragmentation. This range-collapse model is challenged by a new dataset of 406 baiji last-sighting records collected from across the baiji's historical range during an interview survey of Yangtze fishing communities. Although baiji regional abundance may have varied across its range, analyses of the extensive new sighting series provide comprehensive evidence that baiji population decline was not associated with any major contraction in geographical range across the middle–lower Yangtze drainage, even in the decade immediately before probable global extinction of the species. Extinction risk in baiji was therefore seemingly not related to evidence of range collapse. Baiji apparently underwent large-scale periodic and seasonal movements across their range, and we propose that range contraction and fragmentation may not be general biogeographic characteristics for declining populations of mobile species in connected landscapes.

Keywords: *Lipotes vexillifer*; local ecological knowledge; optimal linear estimation; range collapse; time-series data; Yangtze River dolphin

1. INTRODUCTION

Geographical range contraction is one of the fundamental ecological characteristics of species population decline and extinction (Mace *et al.* 2008). Developing a more inclusive understanding of the biogeographic pattern, the temporal rate and the ecological correlates of range collapse across different species groups and regions is a crucial line of research for conservation science. Understanding range collapse more fully will help determine appropriate conservation actions for threatened species, notably enabling the accurate identification and management of 'refugia' where remnant subpopulations may persist after extirpation of individuals across other parts of a historical range. However, in contrast to studies of genetic and life-history factors associated with extinction risk in small and declining populations, relatively little investigation has so far been conducted into the 'dynamic biogeography' of range collapse, beyond the documentation or estimation of historical range contractions experienced by particular species or faunas (cf. Ceballos & Ehrlich 2002; Morrison *et al.* 2007).

The broad taxon-focus analytical studies of Lomolino & Channell (1995) and Channell & Lomolino (2000*a*,*b*) concluded that species typically persist in peripheral isolates rather than core areas of their geographical range, consistent with a 'contagion'-type range-collapse model associated with external anthropogenic impacts rather than a 'demographic'-type model derived from the small-population paradigm (Caughley 1994). Subsequent studies have found varying support for protracted survival of peripheral subpopulations in a range of species (e.g. McShea *et al.* 1999; Doherty *et al.* 2003; Williams *et al.* 2003; Shackell *et al.* 2005). However, there is still little information available on wider biogeographic patterns of range collapse in different taxonomic and ecological groups—such as the relationship between range contraction and fragmentation, and patterns of fragmentation at different spatial scales (cf. Fagan *et al.* 2005)—and general trends remain elusive owing to the complex interplay between species ecology, regional geography and specific threat processes. A fundamental problem involved in understanding spatial patterns of range collapse is that it is necessary to address the full course of an extinction event, from first population decline to final extinction, but this becomes increasingly difficult as rare and declining species become progressively harder to detect. A variety of data sources and analytical approaches may therefore be required to

* Authors for correspondence (samuel.turvey@ioz.ac.uk; hao.yj@ihb.ac.cn).

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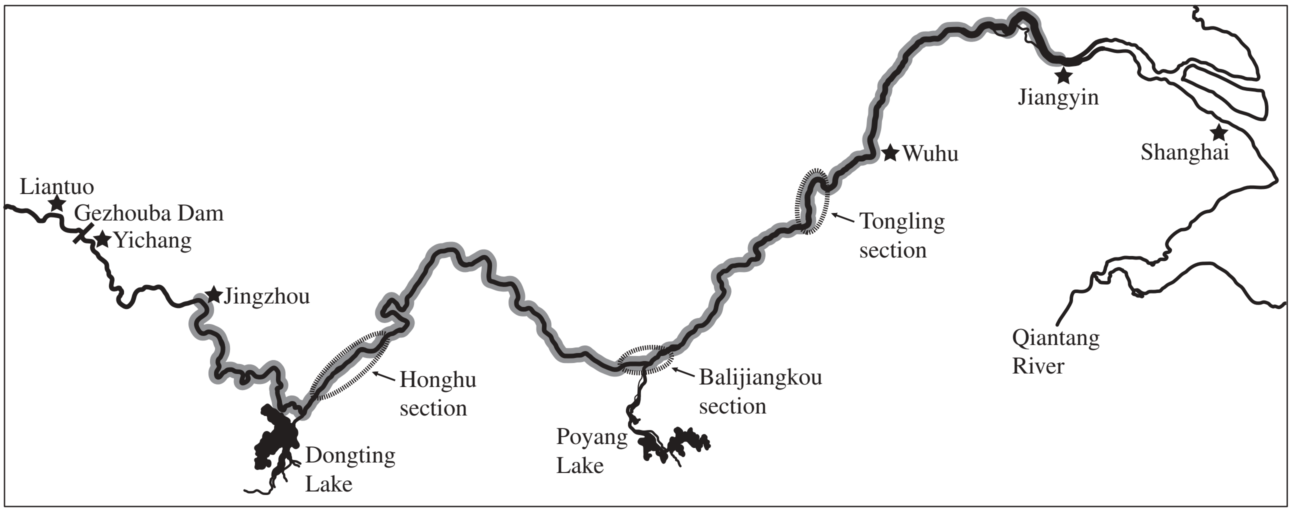

Figure 1. Historical distribution of baiji in the middle–lower Yangtze region. Grey highlighted area indicates baiji distribution by the 1990s inferred from survey data (downstream end of this distribution reconstructed as either Wuhu or Jiangyin by different authors); sections ringed with broken line indicate three supposed remnant baiji 'hotspot' regions at beginning of 21st century; other named locations represent wider distribution of older (mid–late 20th century) baiji records in main Yangtze channel and neighbouring water bodies. See text for further details.

reconstruct patterns of range contraction fully, and it is imperative to obtain accurate distributional time-series data for recently extinct species as a basis for comprehensive studies of dynamic biogeography.

The Yangtze River dolphin or baiji (*Lipotes vexillifer*), an obligate river dolphin from the middle–lower Yangtze region of eastern China, is probably the first large mammal species to have become extinct in over 50 years (Turvey *et al.* 2007). Its decline was driven by incidental by-catch in fishing gear and other factors associated with increasing industrialization of the Yangtze ecosystem (Wang *et al.* 1998; Turvey *et al.* 2007), from approximately 400 individuals in 1979 to as few as 13 individuals by 1997–1999 (Zhou 1982; Zhou *et al.* 1998; Zhang *et al.* 2003). Intensive survey work in 2006 found no evidence of its continued survival (Turvey *et al.* 2007). Baiji historically occurred in the main Yangtze channel, from the estuary to the lower Three Gorges region roughly 1800 km upstream, and also in two large appended lakes (Dongting Lake and, at least transiently, in Poyang Lake) and the neighbouring Qiantang River (Zhou 1958; Zhou *et al.* 1977; figure 1). The baiji's range is believed to have progressively diminished through loss of peripheral subpopulations followed by large-scale range contraction and fragmentation (figure 1). Baiji disappeared from the Qiantang River by 1957, and were reportedly absent from the two lakes by the late 1970s (Zhou *et al.* 1977; Chen 1981, 1986). The species was only recorded in the lower Three Gorges region during the 1940s (Zhou *et al.* 1977), with this peripheral upstream distribution isolated above the Gezhouba Dam since 1981. The baiji's main continuous distribution in the Yangtze channel is also believed to have decreased markedly before its extinction. Zhou *et al.* (1977) and Chen (1986) reported that baiji had recently disappeared from the upstream limit of this distribution around Yichang (1669 km upstream from the river mouth), and by the 1990s survey data were interpreted to suggest that the baiji's range had further contracted by several hundred kilometres to an upstream limit around Jingzhou (1521 km upstream) and a downstream limit near either Jiangyin (157 km upstream) or Wuhu (443 km upstream; Chen *et al.* 1997; Zhang *et al.* 2003). At the beginning of the 21st century it was considered that baiji were generally seen only in the three isolated 'hotspot' sections of Honghu (135 km section), Balijiangkou (40 km section) and Tongling (110 km section; Braulik *et al.* 2005).

This model of baiji range collapse has become accepted in the wider scientific and conservation literature (e.g. Reeves *et al.* 2003; IUCN 2009), and was influential in developing the ultimately unsuccessful baiji recovery programme (Braulik *et al.* 2005; Turvey 2008). However, baiji occurrence data are difficult to interpret owing to substantial variation in survey effort and methods, and a lack of quantitative analysis of survey data. Late sighting records were almost all reported by monitoring networks in hotspot sections, and the predominance of records from these sections may merely reflect a lack of monitoring effort elsewhere along the river (Braulik *et al.* 2005; Turvey *et al.* 2007). It is therefore difficult to use these field data to investigate wider patterns of range collapse in threatened species, or the biogeography of population decline in relation to different ecological parameters.

The baiji's recent distribution and status were further investigated through an extensive interview survey conducted in local fishing communities across the middle–lower Yangtze drainage. Our survey results provide comprehensive evidence that baiji population decline was not associated with any major contraction in distributional range, and also suggest that this biogeographic pattern may be shared with many ecologically similar threatened taxa.

2. MATERIAL AND METHODS

(a) *Interview survey*

Interviews were conducted in 2008 in fishing communities across the middle–lower Yangtze channel and around Dongting Lake and Poyang Lake, at 27 localities covering the entire late 20th century range of the baiji. As part of a wider series of interview questions, informants were asked: their age; the upstream and downstream boundaries of where they went fishing; how many hours per day and days per week they typically spent fishing; whether they had seen baiji; the date and exact location of their most recent baiji sighting; whether they knew of any recent baiji sightings made by other people; and how regularly they saw Yangtze finless porpoises (*Neophocaena phocaenoides asiaeorientalis*), the other cetacean that occurs sympatrically in the middle-lower Yangtze drainage. All informants were required to identify, without prompting, photographic cue cards of live wild and captive baiji and finless porpoises, and dead baiji (taken from Zhou & Zhang 1991; Zhou 2002; provided by the Institute of Hydrobiology), to test their accurate identification of these species and the validity of their responses. For further information about interview protocols, see the electronic supplementary material.

A total of 599 informants were interviewed during the survey. Interview data on baiji last-sighting dates were combined with a limited amount of additional unpublished baiji sighting data obtained from regional fishery authorities, and a small number of documented baiji mortality events from 1995 onwards (Zhang *et al.* 2003; Turvey *et al.* 2007). In total, 406 baiji records (identified as representing separate events owing to differences in date, location and/or other details) were collected for analysis. Special care was taken to verify baiji sighting records from 1995 onwards, with informants required to provide a detailed description of their sighting that was not accepted unless it contained key diagnostic characteristics of baiji (e.g. white colour, long beak). Other previously published baiji distributional sighting data were excluded from our analyses, owing to historical biases in data collection, except in our high-resolution spatial analysis of baiji hotspots (see below).

(b) *Analysis*

Although the majority of baiji sighting dates (51.7%) were reported as direct calendar years, many informants also reported last-sighting dates in alternative formats: paired consecutive calendar years (e.g. '1986/1987'), decadal or other ranges (e.g. '1980s', 'late 1980s'), or decades/half-decades before 2008 (e.g. '20 years ago', '25 years ago'). More recent sighting dates were more likely to be reported as direct calendar years because informants had more accurate recall over shorter time intervals, but in order not to exclude the large amount of additional sighting data from further analysis, dates reported in alternative formats were converted to direct calendar years as follows: paired calendar years were given an equal probability of being assigned to either consecutive year; decadal or other specific ranges were given an equal probability of being assigned to any calendar year from within this range; and dates rounded to a given number of decades or half-decades before 2008 were given an equal probability of being assigned to any calendar year ± 5 the given value (e.g. 20 years ago represents a potential date range from 1983 to 1993).

Although river systems often represent complex landscapes that can be difficult to capture using standard spatial models (Fagan 2002), the baiji's recent historical distribution was largely constrained to the main Yangtze channel, since the river's many tributaries have now either been dammed or otherwise no longer represent suitable cetacean habitat (Liu *et al.* 2000), so that it is possible to investigate baiji spatial population dynamics largely using a straightforward linear framework. The middle–lower Yangtze channel survey transect was divided into seventeen 100 km sections for most analyses, measured according to Yangtze shipping chart river distances from Yichang, with distance of survey section along the Yangtze downstream to the river mouth scored as 1–17 for analysis. Dongting Lake and Poyang Lake were treated as two further independent survey regions. Baiji last-sighting dates and associated informant data were grouped for each 100 km river section and lakes. Informant data were analysed spatially according to the reported fishing distribution of each informant, rather than the locality of the fishing community where that person was interviewed, to give an accurate representation of the geographical scope of informant experience and knowledge. All survey data were analysed in R 2.9.1 (R Project Core Development Team 2009).

General linear models (GLMs) were used to investigate the robustness of the survey data for exploring questions about baiji extinction. The existence of potentially confounding demographic differences between informant groups was tested by examining whether geographical location across the study region predicted differences in the age of informants who fished in each section. Variation in fishing effort, another important demographic variable, has previously been shown to be uncorrelated with informant age or location of the fishing community across the region (Turvey *et al.* in press). The potential for demographic variation and sampling bias to influence regional last-occurrence dates was further investigated by testing whether the date of the most recent baiji sighting recorded in each 100 km section could be predicted by (i) mean age of informants reporting a baiji sighting per section, (ii) mean age of all informants fishing per section, (iii) total number of informants fishing per section and (iv) total number of regional sightings. Although age-related variation in whether informants have encountered baiji and other recently extinct species in the past has been demonstrated in Yangtze fishing communities (Turvey *et al.* in press), we would not expect informant age to have an effect on the timing of recent baiji sightings reported by the subset of informants that have seen the species. This analysis was conducted first using a restricted dataset comprising only sighting data originally reported as direct calendar years, and second using the full dataset (also containing dates secondarily converted to direct calendar years), to test for differences between these two subsets of data. Data were analysed with a binomial error structure and a logit link function (Agresti 1990; Crawley 2007), and the full model is reported in every case. In similar studies, location data (distance) could be considered as ordinal. In this case, we treated data as categorical because of the presence of lakes off the main channel that disrupted the ordinal structure of data.

Optimal linear estimation was used to estimate the date of regional disappearance of baiji across the middle–lower Yangtze from sighting data series for each 100 km river section and the associated lakes (Cooke 1980; Solow 2005; Collen & Turvey 2009). This is a probabilistic approach that uses the temporal distribution of independent, uncorrected sighting events to estimate an extinction date based on the Weibull distribution, a two-parameter model originally used in engineering industrial risk analysis (Crawley 2007). The attraction for an analysis aimed at inferring extinction is that the k most recent sightings can be assumed to have the same Weibull extreme value distribution, regardless of the parent distribution, provided n is large enough (and not necessarily known). We followed Solow's (2005) implementation of the technique. For species with sufficient data (more than five sightings: we used the full sightings record for each section), optimal linear estimation appears to be a useful tool to assess the likelihood of extinction for both regional and global extinctions (Collen *et al.* in press). Although this method relies on the implicit assumption that recording effort never falls to zero (Collen *et al.* in press), the Yangtze region has had an extremely high human population, and 'survey' effort (by fishermen) has been essentially continuous throughout the time period of interest.

Higher-resolution spatial analysis of late baiji sighting records was conducted to further investigate whether the baiji's historical range fragmented into discrete hotspot regions containing clusters of sightings during the period of terminal population decline. The main river channel from Yichang to the estuary was further subdivided into 167 10 km sections, and the exact locations of all sighting records from 1995 onwards were plotted onto these sections, together with all 17 baiji sighting records obtained from the 1997–1999 range-wide baiji surveys (Zhang *et al.* 2003), to record baiji presence/absence in each section. In order to investigate whether the observed level of spatial clustering of these baiji sightings represents a genuine pattern of finer-scale range fragmentation, or merely an artefact of low count numbers, we tested whether the distribution of sightings differs significantly from the null expectation of random assignment along the river channel. Sections were randomized by sampling without replacement using Urn 1.0 (Altman 2007) in R 2.10.0 (R Project Core Development Team 2009) using the observed number of 10 km sections containing baiji sightings versus the total number of sections. The sampling probability was $x/167$ of sighting baiji and $(167 - x)/167$ of not sighting baiji, where x represents the total number of 10 km sections in which baiji were observed. The number of adjacent sections (n) containing sightings was identified using run length encoding, and the mean and standard deviation of n were recorded. This process was repeated one million times. From the distribution of mean n, we calculated the probability of obtaining the observed distribution of sightings if baiji were evenly distributed across the entire region.

Finally, we investigated whether regional variation could be detected across the survey region in past baiji abundance as well as survival. This analysis was based on two assumptions: that both (i) number and (ii) mean (rather than most recent) calendar date of historical baiji sightings recorded per 100 km section represent indices of former relative abundance across the species's range. Variation in past abundance was investigated by testing (i) whether there is significant variation across the region in the proportion of informants fishing per section who have reported a baiji sighting in that section and (ii) whether location across the region can predict the mean sighting date per section. Informant age has already been shown to influence the likelihood that people have seen baiji in the past (Turvey *et al.* in press); to control for this potential confounding variable, we fitted a linear model using age to predict the proportions of informants reporting baiji sightings, and then eliminated the effect of age per section to produce standardized proportions.

3. RESULTS

Fishermen spend a substantial proportion of their lives on the Yangtze (mean fishing effort = 51.1 hr week^{-1}; standard deviation = 27.8; $n = 426$), and are extremely familiar with the status of the river's current-day resources (Turvey *et al.* in press). Although there was inevitable spatial variation across the region in the distribution of human settlements and fishing areas, most informants reported that they travelled substantial distances up- and downstream on a regular basis when engaged in fishing activities, with 57–149 informants regularly fishing in or travelling through each of the 100 km survey sections. We are therefore confident that our interviews captured detailed spatial observation data across the entire late 20th century range of the baiji.

Table 1. Results of general linear models used to determine effect of (i) total number of regional baiji sightings, (ii) total number of informants fishing per section, (iii) mean age of informants reporting baiji sightings per section and (iv) mean age of all informants fishing per section, on dates of most recent baiji sightings recorded per 100 km section. Analysis conducted on restricted dataset comprise only sighting data originally reported as direct calendar years; full dataset also contains dates secondarily converted to direct calendar years.

predictor	error d.f.	F ratio	p
restricted dataset			
mean age of informants who have seen baiji per section	1,13	0.001	0.971
mean age of all informants fishing per section	1,13	1.152	0.303
total number of informants fishing per section	1,13	1.973	0.184
total number of regional baiji sightings	1,13	4.242	0.060
full dataset			
mean age of informants who have seen baiji per section	1,13	0.033	0.859
mean age of all informants fishing per section	1,13	1.488	0.244
total number of informants fishing per section	1,13	3.304	0.092
total number of regional baiji sightings	1,13	1.440	0.252

Only 9.9 per cent of informants reported that they had not seen finless porpoises in 2008, or had only seen them 'in the past' ($n = 563$). However, only 60.1 per cent of informants had ever seen baiji ($n = 591$). Most of these informants had not seen any baiji for decades (mean last-sighting date using entire dataset = 1985; mean last-sighting date using only direct calendar year data = 1987). Only 8.1 per cent of baiji last-sighting records ($n = 33$) date from 2000 onwards (i.e. after the final official baiji survey that detected dolphins; electronic supplementary material). The numbers of 21st century reports also tail off markedly over time, with almost half of these final sightings (15/33) reported from 2000 to 2001, suggesting that the remnant baiji population still present at the start of the 21st century continued to decline rapidly.

Informant age is significantly correlated with geographical section across the survey region, indicating that potentially confounding demographic differences exist between informant groups ($F_{18,1596} = 4.872$, $p < 0.001$). However, these age differences do not bias recent baiji last-sighting dates recorded across the region: the most recent sighting date recorded from each 100 km section is not significantly correlated with either mean age of informants who had reported sightings per section, or mean age of all informants fishing per section (table 1).

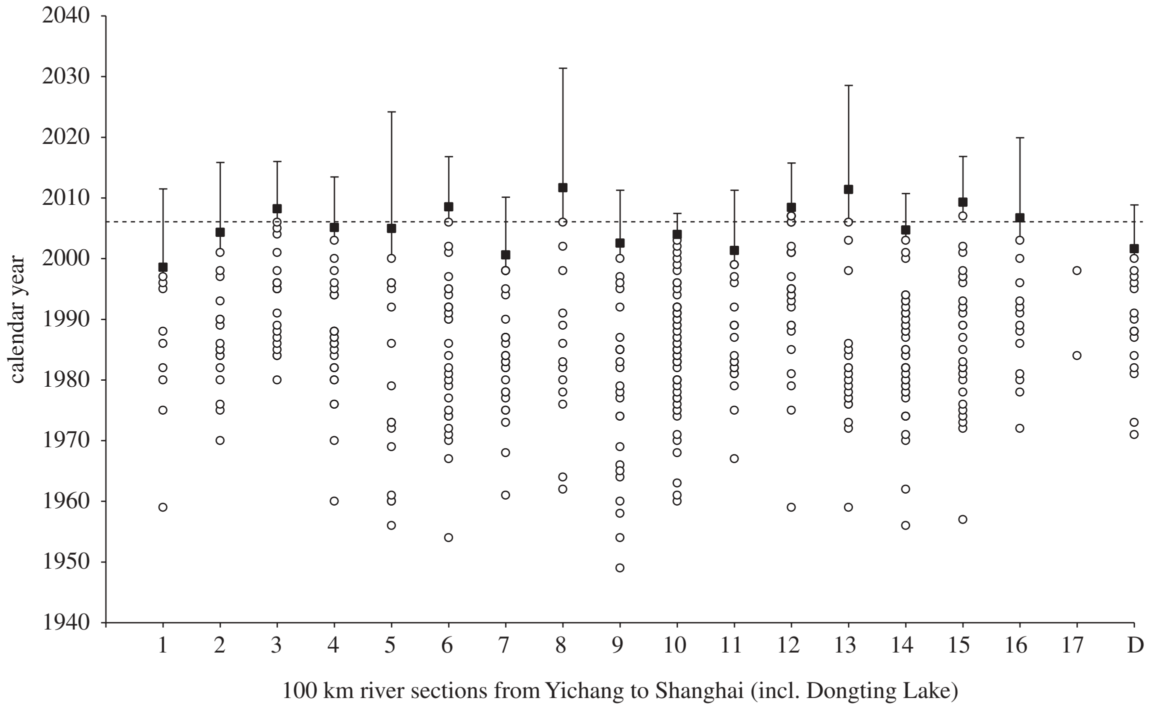

Figure 2. Temporal distribution of baiji last-sighting dates across the seventeen 100 km Yangtze river sections from the Yichang section (1) downstream to the estuary (17), and from Dongting Lake (D), showing 95% confidence intervals for optimal linear estimation of regional extinction date for all sections with sufficient sighting data series. Baiji sightings dating from 1997 or later were reported from all of these sections, and all optimal linear estimation confidence intervals overlap 2006 (dotted line), the calendar year in which the baiji is inferred to have become extinct (Turvey *et al.* 2007).

The date of the most recent sighting per section also does not show a significant relationship with either number of regional sightings ($n = 1-52$) or total number of informants fishing per section, indicating that regional baiji last-occurrence dates are not affected by sampling error and are relatively robust (table 1). The same pattern is shown by both non-randomized and randomized sighting data series.

No baiji sightings were reported by informants from Poyang Lake, supporting the hypothesis that baiji disappeared from the lake several decades ago or may have been only a transient visitor (Zhou *et al.* 1977; Chen 1986). This region was therefore excluded from further analysis. In contrast, baiji sightings dating from 1997 or later were collected from every 100 km river section and Dongting Lake (electronic supplementary material), indicating that baiji still occurred across the entirety of their contiguous historical range in the main Yangtze channel between Yichang and the estuary, as well as in one of the major appended lakes, until less than a decade before their probable global extinction. Sufficient baiji sighting series were available to conduct optimal linear estimation of extinction date for sixteen of the seventeen 100 km river sections and Dongting Lake; only two baiji sightings were reported from the seventeenth river section, including a verified stranding in 1998. Our 95 per cent confidence intervals for each estimated regional extinction date overlap 2006, the calendar year in which the baiji is inferred to have probably become extinct (Turvey *et al.* 2007), indicating that there is no statistical support for temporal variation in regional disappearance of baiji (i.e. range contraction or fragmentation) from anywhere across this range (figure 2).

When the main river channel is divided into 167 10 km sections, 47 sections contained a baiji sighting record from 1995 onwards, distributed from Yichang to Chongming Island in the river mouth (figure 3). The observed distribution of sighting records during this terminal period falls within the distribution of simulated random assignment for 47 sightings across the main Yangtze channel. There is therefore no evidence for baiji population fragmentation or clustering of sighting data during the period of terminal population decline even at this higher-resolution spatial scale (figure 4).

Whereas our last-sighting data provide no evidence for range contraction or fragmentation, they do suggest that baiji abundance varied across its range in the decades before its extinction. There is significant variation across the survey region in both of our inferred measures of baiji abundance, i.e. proportions of informants who have reported baiji sightings per section ($\chi^2 = 77.437$, d.f. $= 17$, $p < 0.001$) and mean calendar date of historical baiji sightings recorded per section (GLM: $F_{17,387} = 3.43$, $p<0.001$; figure 5). Peaks in both of these measures across the survey region show some congruence with previously identified hotspots, suggesting that these may have represented areas of historically higher baiji abundance. However, several non-hotspot sections also show high informant sighting proportions, notably the downstream Nanjing–Zhenjiang section (sections 14 and 15). Informant sighting proportions also suggest that baiji may have displayed decreasing abundance at range margins, a first step towards range contraction, as the Yichang and estuary sections (sections 1 and 17) show low levels of inferred abundance.

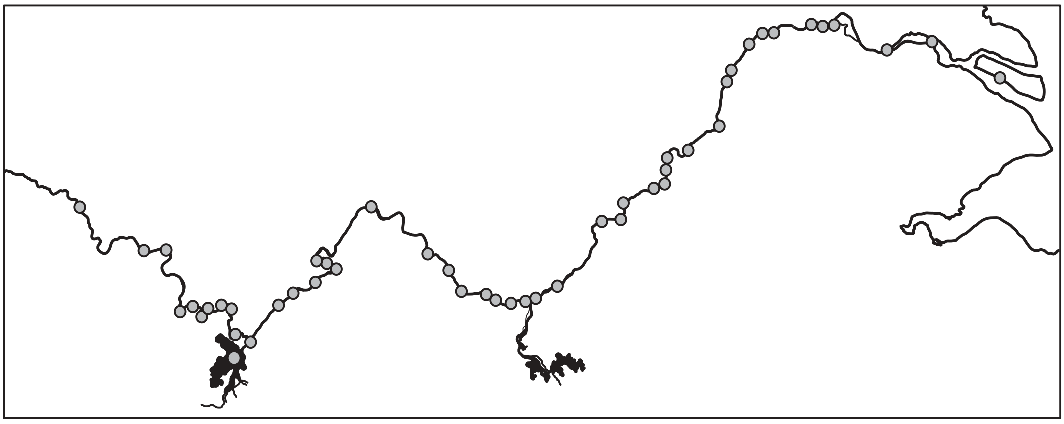

Figure 3. Distribution of baiji sighting records across the middle–lower Yangtze region dating from 1995 onwards (representing 47 10 km river sections in the main Yangtze channel as well as Dongting Lake).

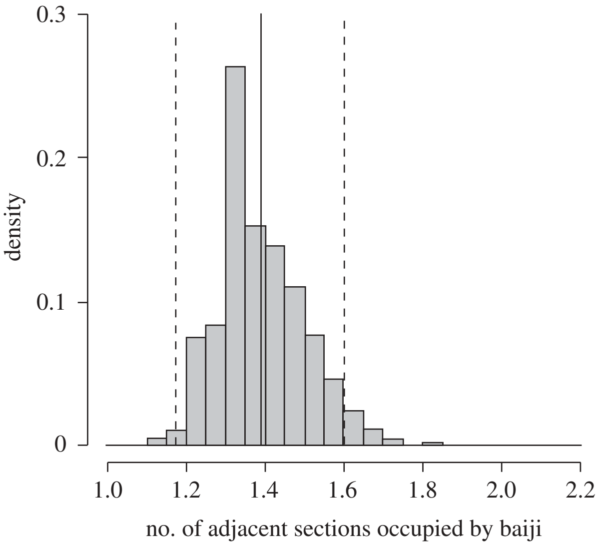

Figure 4. Density histogram of simulated means of observed spatial clusters of geographically adjacent sightings, drawn from randomized distribution of 47 sighting events across 167 contiguous 10 km river sections, with 1.96 standard deviations from the mean shown by dashed lines. Solid line indicates the mean for the observed number of adjacent 10 km river sections occupied by baiji from 1995 onwards.

4. DISCUSSION

The primary aim of our survey was to investigate the possible continued persistence of baiji in the Yangtze. Although a small number of sightings were reported from recent years, most informants have not seen baiji for several decades, and we found little evidence that the species still survives. However, the geographical pattern of late baiji sightings challenges previous models of baiji range collapse, since our analyses of the extensive new sighting series dataset provide comprehensive evidence for a lack of any major range contraction or fragmentation in the main Yangtze channel, or for early disappearance from Dongting Lake, even in the decade immediately preceding probable global extinction of the species. At most, there is evidence for decreased former abundance (but continued presence) of baiji at the upstream and downstream ends of their historical distribution in the Yangtze channel. There is also no evidence for scale-dependent range fragmentation, even at a high-resolution 10 km scale (cf. Fagan *et al.* 2005), and several post-1995 baiji reports were even collected from major urbanized centres along the middle–lower Yangtze, notably from river islands in the Wuhan and Nanjing sections associated with favourable countercurrent environments (cf. Hua *et al.* 1989).

The use of anecdotal occurrence data to establish historical presence and distribution of cryptic or recently extinct species may be vulnerable to inaccuracy, owing to the potential for reporting error and bias (e.g. poor identification or recollection; informant reticence, overeagerness or integrity; McKelvey *et al.* 2008; Papworth *et al.* 2009). However, we are confident that the new baiji sighting data are largely accurate. Integrity of informants across the survey region has been demonstrated by congruence between geographical variation in their responses about the status and abundance of threatened fish species with independently derived field data (Turvey *et al.* in press). Accurate identification of baiji and recall of past baiji sightings by informants were specifically tested by the interview design (e.g. unprompted cue card identification; requirement for key diagnostic baiji characteristics accompanying sighting reports), and the huge difference in number and date of reported sightings of baiji and finless porpoises indicates that informants were able to discriminate accurately between these two cetaceans. Mistakes in recall of sighting dates cannot be ruled out, but such mistakes can be assumed to be proportionally equivalent rather than geographically biased across the survey region, and more recent sighting dates (of primary interest for our survey) are considered most likely to be remembered accurately. The temporal distribution of baiji last-sighting data and relatively limited number of recent sighting dates also show close correspondence with independent estimates of baiji population decline based on survey data (Zhou *et al.* 1998; Zhang *et al.* 2003; Turvey *et al.* 2007), further supporting the general accuracy of informant memory of the timing of baiji sightings.

Our new model of the dynamic biogeography of baiji extinction provides important insights into the wider relevance of the range contraction and range fragmentation paradigms of extinction under differing ecological conditions. Although relatively little scientific information about baiji ecology or population movement was collected before the probable extinction of the species,

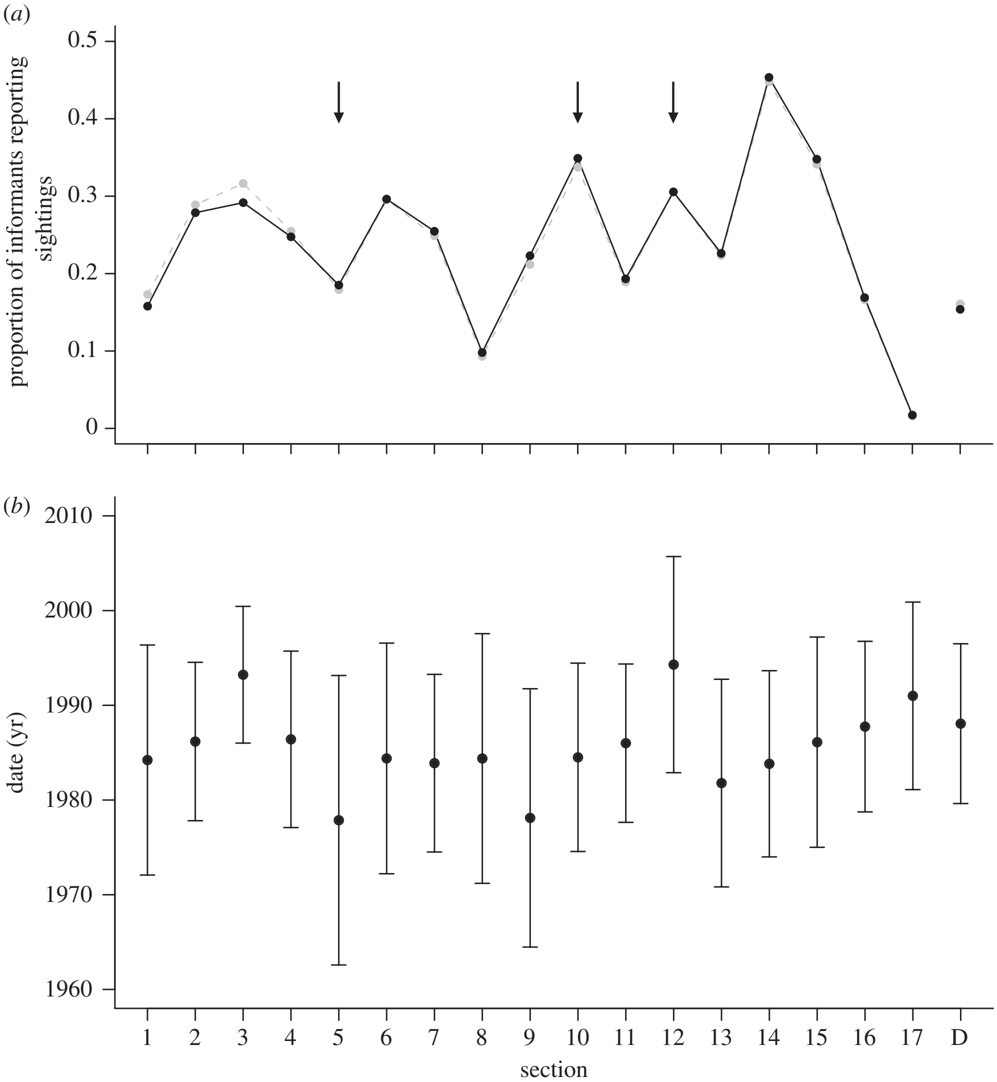

Figure 5. Two indices of inferred historical variation in abundance of baiji across the seventeen 100 km Yangtze river sections from the Yichang section (1) downstream to the estuary (17), and in Dongting Lake (D). (*a*) Proportions of informants fishing per section who have reported baiji sightings from that section. Raw proportion data shown by black circles and solid line; age-standardized proportion data shown by grey circles and dashed line. Arrows indicate location of supposed remnant baiji 'hotspots' at the beginning of the 21st century. (*b*) Mean calendar date of historical baiji sightings recorded per section.

photo-identification studies found evidence of long-range individual baiji movements over distances of more than 200 km (Zhou *et al.* 1998). Anecdotal information previously collected from fishermen also suggests that baiji made large-scale seasonal movements up and down the main Yangtze channel and into Dongting Lake (Hoy 1923; Zhou *et al.* 1977; Zhang *et al.* 2003). Despite the extensive ongoing industrialization and development of the middle–lower Yangtze drainage, there are still no major barriers to long-distance movement for mobile or migratory aquatic species across this system downstream of Yichang. It is therefore possible that such periodic and seasonal movements allowed the final remnant baiji population to continue dispersing across the entirety of this contiguous historical distribution, even during its terminal decline, when the population numbered in the tens of individuals at most. This suggests that range contraction and fragmentation may not be general biogeographic characteristics for mobile species in connected landscapes, even when such species are highly threatened.

Although earlier identification of supposed baiji hotspots was largely based on geographically biased data, our range-wide analyses support the suggestion that baiji abundance varied across the survey region. Our quantitative interview-based approach to investigating relative abundance patterns may therefore represent a potentially useful tool for the cost-effective spatial allocation of conservation resources for other threatened species. However, the new model of the dynamic biogeography of baiji extinction suggests that conservation strategies to establish unconnected river sections as discrete *in situ* baiji reserves (Chen & Hua 1989; Zhou *et al.* 1994, 1998) may not have been consistent with the ecological requirements of the species, although in practice it was probably not possible to establish effective protection of large contiguous river sections in the densely populated Yangtze drainage (Wang *et al.* 2006). Similar problems are also faced in conservation efforts for other threatened species that range beyond the borders of protected areas (Woodroffe & Ginsberg 1998; Collen *et al.* 2006). This model also has major implications for understanding range change and identifying appropriate conservation strategies for other freshwater cetaceans, which represent the world's most threatened group of large mammals (Reeves *et al.* 2000, 2003). Significantly, in contrast to the baiji, mtDNA genetic structuring shown by finless porpoises from across the middle–lower Yangtze has been interpreted to suggest that these animals do not move far (Zheng *et al.* 2005), and recent surveys have reported an apparent geographical gap in their formerly contiguous distribution in combination with severe ongoing population decline (Zhao *et al.* 2008). Further investigation of population movements and apparent range fragmentation in Yangtze finless porpoises, together with implementation of ecologically appropriate conservation actions, should be a priority for this endangered cetacean.

More fundamentally, extinction risk in baiji was seemingly unrelated to evidence of either range contraction or fragmentation. Changes in the status of these two components of a species's geographical range are among the standard criteria used by the International Union for Conservation of Nature (IUCN 2001) to assess threat status, under criterion B (B1: extent of occurrence; B2: area of occupancy), because species are considered to be at higher risk of extinction if they have small, declining and/or fragmented distributions. Of the 17 291 species currently assessed as threatened (Vulnerable, Endangered or Critically Endangered), 52.3 per cent have been assigned this status partly or entirely on the basis of criterion B (IUCN 2009). The spatial extinction dynamics exhibited by the baiji suggest that range change in threatened species can be determined by intrinsic factors associated with species biology and autecology, as well as by more widely acknowledged extrinsic threat processes. Our evidence suggests that in the case of this species, both extent of occurrence and area of occupancy apparently remained high and virtually unchanged until close to the time of extinction. Other migratory or otherwise highly mobile species may therefore also not be expected to exhibit any significant change in range extent or range occupancy even up to the time of extinction. We propose that an organism's migratory or dispersion ability may represent a key determinant of both the pattern and extent of range change in declining populations, at least for populations with contiguous geographical ranges. This hypothesis should be addressed in future analyses of dynamic biogeography.

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