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Global population collapse in a superabundant migratory bird and illegal trapping in China

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Abstract: *Persecution and overexploitation by humans are major causes of species extinctions. Rare species, often confined to small geographic ranges, are usually at highest risk, whereas extinctions of superabundant species with very large ranges are rare. The Yellow-breasted Bunting (*Emberiza aureola*) used to be one of the most abundant songbirds of the Palearctic, with a very large breeding range stretching from Scandinavia to the Russian Far East. Anecdotal information about rapid population declines across the range caused concern about unsustainable trapping along the species' migration routes. We conducted a literature review and used long-term monitoring data from across the species' range to model population trend and geographical patterns of extinction. The population declined by 84.3–94.7% between 1980 and 2013, and the species' range contracted by 5000 km. Quantitative evidence from police raids suggested rampant illegal trapping of the species along its East Asian flyway in China. A population model simulating an initial harvest level of 2% of the population, and an annual increase of 0.2% during the monitoring period produced a population trajectory that matched the observed decline. We suggest that trapping strongly contributed to the decline because the consumption of Yellow-breasted Bunting and other songbirds has increased as a result of economic growth and prosperity in East Asia. The magnitude and speed of the decline is unprecedented among birds with a comparable range size, with the exception of the Passenger Pigeon (*Ectopistes migratorius*), which went extinct in 1914 due to industrial-scale hunting. Our results demonstrate the urgent need for an improved monitoring of common and widespread species' populations, and consumption levels throughout East Asia.*

Keywords: extinction, illegal hunting, population model, population trend, Southeast Asia, Vortex, wildlife consumption, Yellow-breasted Bunting *Emberiza aureola*

El Colapso de la Población Global de un Ave Migratoria Superabundante y la Captura Ilegal en China

Resumen: *La persecución y la sobreexplotación por parte de los humanos es una de las principales causas de la extinción de las especies. Las especies raras, generalmente confinadas a extensiones geográficas pequeñas, usualmente tienen mayor riesgo, mientras que las extinciones de especies superabundantes con extensiones*

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*amplias son poco comunes. El escribano de pecho amarillo (*Emberiza aureola*) era una de las aves canoras con mayor abundancia en la zona Paleártica, con un área de reproducción muy grande que se extendía desde Escandinavia hasta el extremo oriental de Rusia. La información anecdótica sobre la declinación rápida en esta extensión causó preocupación por la captura insostenible a lo largo de las rutas migratorias de la especie. Realizamos una revisión bibliográfica y usamos datos de monitoreo a largo plazo de toda la extensión de la especie para modelar la tendencia poblacional y los patrones geográficos de extinción. La población declinó en un 84-3–94.7% entre 1980 y 2013, y su extensión se redujo en 5000 Km. La evidencia cuantitativa de las redadas policiales sugiere una rampante captura ilegal de la especie a lo largo de su ruta de vuelo en China. Un modelo poblacional que simulaba un nivel de captura inicial del 2% y un incremento anual del 0.2% durante el periodo de monitoreo produjo una trayectoria poblacional que igualó a la declinación observada. Sugerimos que la captura contribuyó fuertemente a la declinación, ya que el consumo del escribano de pecho amarillo y otras aves canoras ha incrementado como resultado del crecimiento económico y de la prosperidad en el este de Asia. La magnitud y la velocidad de la declinación no tiene precedentes entre las aves con un tamaño de extensión comparable, con la excepción de la paloma pasajera (*Ectopistes migratorius*), la cual se extinguió en 1914 debido a la cacería de nivel industrial. Nuestros resultados demuestran la necesidad urgente de un monitoreo mejorado de las poblaciones de especies comunes y con extensiones amplias y de los niveles de consumo a lo largo del este de Asia.*

Palabras Clave: cacería ilegal, consumo de vida silvestre, escribano de pecho amarillo, extinción, modelo poblacional, sureste asiático, tendencia poblacional, Vortex, *Emberiza aureola*

Introduction

Human-induced extinction rates are currently about 100–1000 times natural background rate and are predicted to increase (Pimm et al. 1995). Extinction risk varies among species. Specialized and rare species with small ranges that inhabit islands or occur at low densities are most vulnerable (Cardillo et al. 2005; Kotiaho et al. 2005) because they are most sensitive to natural disasters, disease, and human disturbance (McKinney 1997). Human-induced extinctions and declines to near-extinction of superabundant species with extremely large ranges are rare. A traditional focus in conservation biology has been on rare species because of their often more imminent extinction risk (Lindenmayer et al. 2011). Common species are often considered safe. However, recent evidence suggests that widespread losses in common species might be an underrated conservation problem (Inger et al. 2015).

Human activities associated with land-use changes, such as agriculture and forestry, or climate change, are commonly considered major drivers of biodiversity loss (Vitousek et al. 1997). Direct persecution of species plays a less important role in industrialized countries, but it is still a persistent threat in the developing world (Rosser & Mainka 2002; Warkentin et al. 2009). Especially in East Asia, where the consumption of wildlife products for medical, superstitious, and nutritional reasons is culturally rooted and widespread (Sodhi et al. 2004; Nijman 2010), hunting and overexploitation are major causes of species extinctions (Yiming & Wilcove 2005). Persecution pressure is well studied for enigmatic and conspicuous species in East Asia (e.g., Gao & Clark 2014; Liu & Weng 2014), but little is known about the effect of large-scale trapping and consumption on abundant and widespread terrestrial biodiversity (Sodhi et al. 2004; Yong et al. 2015). Most studies have examined the effects of trapping only on a local level (Liang et al. 2013). Furthermore, many of East Asia's countries have seen recent disproportionate human population and economic growth. The interactions between growth, prosperity, and traditional wildlife consumption habits and species endangerment are poorly understood.

The Yellow-breasted Bunting (*Emberiza aureola*) used to be one of the most abundant songbirds in the northern Palearctic region; their breeding distribution of 15.7 million km^2 stretched from Finland in the west to the Pacific coast in the east (BirdLife International 2014) (Fig. 1). The species has been described for large parts of its range as being superabundant. Large-scale local population densities can be very high (approximately 1 singing male/ha over vast areas of Siberia [Rogacheva 1992]) and indicate that populations likely consisted of hundreds of millions of birds during the 1980s. Yellow-breasted Buntings from across their breeding range migrate eastward to China (Glutz von Blotzheim & Bauer 1997) and winter in Southeast Asia. Both during migration and in winter, they congregate in large flocks in wet grasslands and rice fields, including at numerous stopover sites in China (Glutz von Blotzheim & Bauer 1997). Since the late 1990s, there has been growing anecdotal evidence of widespread local extinctions and rapid declines of the species across its range (Chan 2004; Yong et al. 2015). This resulted in an increasingly less favorable conservation status: 2004, near threatened (BirdLife International 2004); 2008: vulnerable, 2014: endangered (BirdLife International 2014). However, a range-wide trend has never been quantified.

During migration and on the wintering grounds, Yellow-breasted Buntings gather in huge flocks at roosts. In China, and to a lesser extent in Thailand

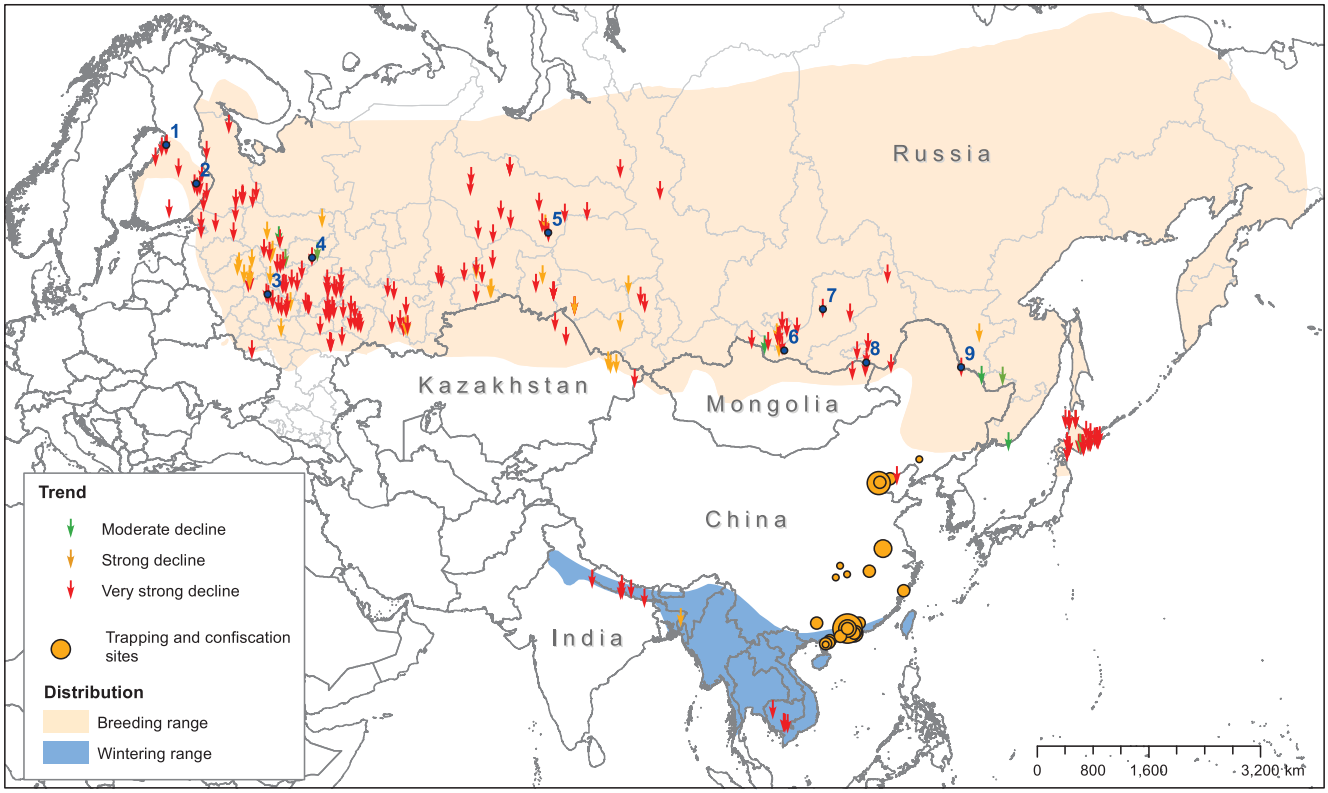

Figure 1. Spatial distribution and magnitude of population declines and illegal trapping incidents for Yellow-breasted Bunting (orange dots, sites where large quantities of these buntings were confiscated, dot size scaled to the number of confiscated birds, range 100–120,000; dark blue circles, sites from which monitoring and survey data were used to calculate the population trend; site numbers correspond to those in Supporting Information (source of the distribution map: BirdLife International distribution database).

and Cambodia, birds have traditionally been trapped at migration roosts with mist nets for food (Glutz von Blotzheim & Bauer 1997). Following initial population declines, the food trade in the species was outlawed in China in 1997, but ongoing illegal trade along the entire Chinese flyway continued because a large black market exists for Yellow-breasted Buntings and other songbirds. For 2001, Chan (2004) estimated a total of 1 million bunting were consumed in China's Guangdong province. Concerns have been raised that trapping levels may be unsustainable and may have increased in recent years due to an increased demand in China, caused by population and economic growth.

For 1980–2013, we reviewed published and unpublished data from 237 sites across the breeding and wintering range and used unpublished monitoring data to establish a global population trend and geographical patterns of decline. We evaluated the extent of illegal trade in the species, based on quantitative information on confiscated birds from police raids in China. By comparing projected population trajectories resulting from different scenarios in a population model, we evaluated whether plausible harvest levels and potential alternative causes are consistent with the observed decline.

Methods

Literature Review

For 1980–2013, we searched for published and unpublished information on local trends in Yellow-breasted Bunting populations. Addition to standard internet search engines and services such as Google Scholar and Web of Science, we included web libraries in Russian and Chinese in our search, notably the Russian language database http://www.elibrary.ru. Red data books from all provinces of the Russian Federation (available online from http://oopt.aari.ru/bio/8672) were also searched. Additionally, internet resources such as websites, blogs, and mailing lists from areas across the range of the species were searched. Russian, Kazakhstani, and Mongolian ornithologists were approached opportunistically by email and asked to provide unpublished data from their areas on population sizes or densities over longer periods. We also included information on the conservation status of the species posted at Birdlife International's Globally Threatened Bird Forums (www.birdlife.org/globally-threatened-bird-forums/). We searched online resources for the species name in English, for its scientific name (including the invalid synonym *Ocyris aureola*, which is

still widely used in Russia), and for its name in the respective country languages. Combinations of the species name with *trend*, *change*, *population*, *number*, *decline*, *stable*, and *increase* were also entered.

Where available, we extracted abundance and density estimates together with location and time of the estimate. Often only anecdotal evidence was available that suggested changes in population. Descriptive information (e.g., changes from common, very common, or very abundant to much rarer, very rare, almost disappeared, stable, or extinct) was noted with the year of the survey. In total, information on population changes was available for 237 sites that could be identified on maps and geo-referenced with sufficient detail (225 sites on the breeding range and 12 across the wintering range). The availability of information was biased toward European Russia and southern Siberia and the Russian Far East. There might be stable populations in the regions not covered by our analyses, but we considered this unlikely because declines were noted across the entire wintering range of the species. Also, negative population trends are more often published than positive or stable trends in order to raise awareness for conservation. This bias may have led to an overestimation of the overall magnitude of decline. However, because we not only searched sources that were directly related to Yellow-breasted Bunting but also reviewed many species lists with abundance estimates for all bird species in a certain area and local descriptions of bird communities, we thought it unlikely that there were many regions where Yellow-breasted Bunting numbers were stable or increased from 1980 to 2013.

We classified all available information on population changes according to the following criteria. Where quantitative data (index counts or density estimates) were available from at least 2 years that were at least 10 years apart, we calculated the difference between these estimates and classified changes of >90% as very strong decline, changes of >50% as strong decline, and changes of >30% as moderate decline. Where only anecdotal information was available (e.g., very abundant in period 1 and rare in period 2), we qualitatively categorized the rate of decline (Supporting Information).

Compilation of Trapping Data

After trapping of the species became illegal in China in 1997, the police searched markets, trains, and transport vehicles for Yellow-breasted Buntings. Successful raids were often reported in the press and on internet sites. To gain an overview about the magnitude and geographical pattern of illegal trapping in China, we compiled information on trapped and confiscated birds for 2000–2014 by searching the internet and printed media (Supporting Information). We were only able to include incidents of illegal trapping that were discovered, reported to the police, and subsequently published by the media. The number of confiscated birds hence provided a conservative index of the magnitude of illegal trapping and it does not necessarily correlate to the total number trapped because police effort, reporting, and media interest varied among years.

Analysis of Monitoring and Survey Data

To quantify the magnitude of population change and detect temporal patterns, we analyzed long-term monitoring data and repeat surveys from 9 sites that were spread from the western to the eastern margin of the distribution range (i.e., from eastern Finland to the Amur area in the Russian Far East) (Fig. 1 & Supporting Information). At the sites in Finland and European Russia, territory mapping was used to estimate abundance for the surveyed areas. In one area in Finland and at the southern end of Lake Baikal, we pooled counts from 3 and 4 subsites that were situated near each other to avoid problems with pseudoreplication. At the sites in Siberia and the Russian Far East, counts were conducted along walked transects of a defined strip width, and population densities were calculated as the number of singing males per square kilometer. These transects were in all types of land cover and were repeated at the same time of the year (from late May to mid-June, corresponding to peak breeding activity of the species). At 2 sites in Finland and 1 site near Moscow, territorial pairs of Yellow-breasted Bunting were surveyed annually between the early 1980s and 2–5 years after the year of the last observation. At all other sites, surveys were not conducted annually and occurred during the breeding period.

We derived annual indices of population size by modeling abundance as a function of year. We used generalized linear mixed models (GLMMs) with a Poisson error structure and a log link in package lme4 in R (version 3.0.2). Raw counts of singing males or pairs were used as the dependent variable for sites where territory mapping was conducted. Where densities (in singing males per square kilometer) were estimated from line transect surveys, all values were converted into count data by multiplying them with different area values. We used 3 different area sizes to test the sensitivity of the resulting trends to the area size used, namely 1, 10, and 100 km^2. Site was fitted as random factor and year as a fixed factor. Parameter estimates for year were then extracted, standardized, and used as indices for population size in a given year over all sites. To control for overdispersion, we fitted an additional observation-level random effect. Model fit was assessed by the marginal R^2 of Nakagawa and Schielzeth (2013), which is interpreted as the variance explained by the fixed factors of the model.

To calculate an overall, range-wide population trend, a generalized additive model (GAM) with a Gaussian error structure and a cubic spline smoother value of $k = 3$ (in R package mgcv) (Wood 2006) was used to smooth the

time series of annual indices. The population index was modeled as a function of year. Annual percent change in abundance and an estimate for total population decline over the 34-year period were ultimately calculated from predicted model values.

Correlates of Local Extinction Time

For 86 sites (38.2%) identified in the literature review, the approximate year of local extinction was given in the sources. From a first screening of the local extinction times, we anticipated that the species vanished from the west to the east of the range, suggesting a retraction to its biogeographical origin in the eastern Palearctic. We used a similar GAM as described above to relate extinction times of sites with known extinction years from the western and central parts of the range to latitude and longitude. Because extinction time might also have been influenced by habitat, we included land cover as a proxy for habitat as a fixed factor in the models. Values for land cover were extracted from Globcover 2009, a global land cover classification (Olson et al. 2001). We forced human population density as a (unsmoothed) covariate into all models to correct for the fact that bunting declines in areas of dense human population might have been detected earlier. Values from the year 2000 were used and extracted from a global raster database with 0.5° resolution (CIESIN 2000). Models containing all possible combinations of variables were compared by Akaike's information criterion for small sample sizes (AIC_c). Models with $\Delta AIC_c < 2$ from the model with the lowest AIC_c were considered equally informative and to have substantial support.

Exploring Potential Causes of the Population Collapse

Population declines can be caused by various factors, most prominently habitat loss or increases in mortality due to persecution or environmental pollution. Because we had no direct evidence that harvest in China caused the population collapse of Yellow-breasted Buntings, we estimated the population trajectory of the species under 4 different scenarios that reflected plausible large-scale environmental changes. We used a population viability analysis to explore the population trajectory under each scenario and to test whether the observed population decline was consistent with realistic expectations of harvest levels. We first specified a baseline simulation that included life-history traits and information on reproductive rates and mortality of stable populations. Values for all parameters were available for Yellow-breasted Bunting from the literature except mortality estimates for first year and adult birds (Supporting Information). We therefore used mortality values for the ecologically close migratory Reed Bunting (*Emberiza schoeniclus*) from a robust study in Europe. We assumed no inbreeding depression, an adult sex ratio of 1:1, and no population catastrophes (abrupt loss of individuals). We then contrasted the baseline model with 4 alternative scenarios representing plausible causes for the population decline. Our harvest scenario contained a function simulating harvest of individuals on a regular basis, and we hypothesized that trapping had been widespread before the population declined and increased recently due to increasing demand and consumption. We used values of 1%, 2%, and 5% of the population harvested in the starting year and a subsequent annual increase of 0.1%, 0.2%, and 0.5% of individuals trapped until the last simulation year. In our second scenario (habitat scenario), we assumed increasing habitat loss caused the population collapse. Under this scenario, the carrying capacity for the species (representing available habitat) was reduced annually by 10%, 20%, and 50% in the model. In our third scenario, we assumed environmental pollution caused disease or sublethal poisoning (pollution scenario) and led to gradual increases in mortality. We simulated this scenario by increasing adult and first year mortality by 5%, 10%, and 15%, based on observed survival differences of stable and increasing or decreasing populations in a study considering a large number of songbird species (Siriwardena et al. 1998). For the fourth scenario, habitat loss and environmental pollution occurred simultaneously, and we combined the effects of the habitat and pollution scenarios by reducing carrying capacity and increasing mortality in the simulations.

We simulated Yellow-breasted Bunting population dynamics under these different scenarios in program Vortex 10.0. Vortex is an individual-based, deterministic simulation program that can accommodate the effects of demographic, environmental, and genetic stochastic events on wildlife populations (Lacy 1993). Each simulation was specified for a hypothetical population size of 100 birds and run 100 times over 34 years, corresponding to the period for which monitoring data were available.

Results

From 1980 to 2013, very strong declines were recorded at 82.5% of the identified breeding and wintering sites and strong declines were recorded at 13.8% of the sites identified in the literature review (Fig. 1). No evidence was found for stable populations after the year 2000 across the breeding and wintering ranges from the literature review. Very strong declines were also noted across the entire wintering range (e.g., in Nepal and Bangladesh since the year 2000 and in Cambodia since about 2005) (Fig. 1).

The range-wide population trend based on re-surveys and annual monitoring data from 9 sites was sensitive to the area that was used when converting densities from line transect surveys to abundance values (Fig. 2).

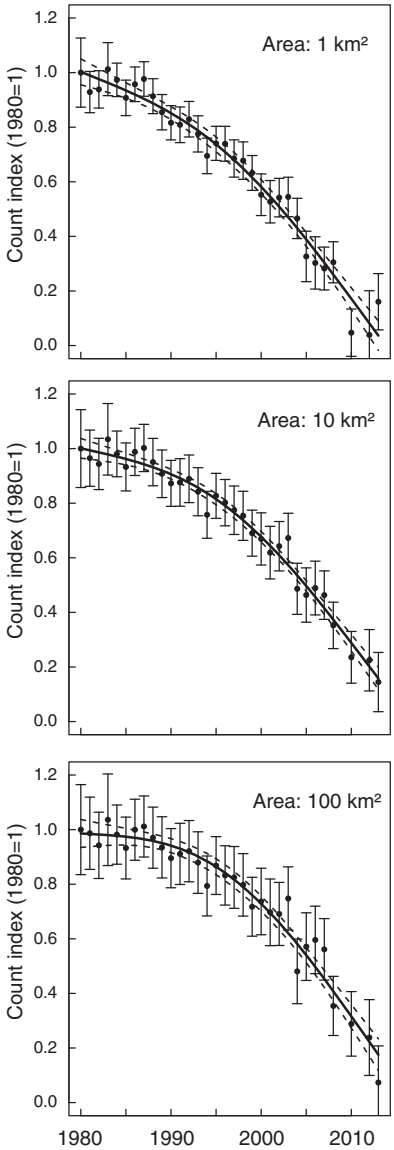

Figure 2. Range-wide population trend of Yellow-breasted Bunting 1980–2013 calculated from monitoring data collected at 9 sites across the range (Fig. 1 & Supporting Information). Modeled annual abundance indices from a generalized linear mixed model are shown (standardized to 1980 = 1) (solid line, smoothed trend over the entire period; dashed line, predicted values from a generalized additive model; vertical lines, parametric 95% confidence interval). Three alternative trend curves from 3 models are plotted to illustrate the sensitivity of the trend estimation to a varying area size when converting density estimates into abundance values.

A conversion based on a survey area size of 100 ha (1 km²) yielded a prediction of a 94.7% decline from 1980 to 2013 (GLMM [annual indices]: marginal $R^2 = 0.847$; GAM [smoothed trend]: adj. $R^2 = 0.97$, $P < 0.001$); the decline was estimated as 84.3% based on 10 km² area (GLMM: marginal $R^2 = 0.744$; GAM: adj. $R^2 = 0.98$, $P < 0.001$) and as 87.2% for 100 km² area (GLMM: marginal $R^2 = 0.744$; GAM: adj. $R^2 = 0.95$, $P < 0.001$). However, the general pattern suggested by the models was similar; the population was rather stable until around 1987, when a strong decline started (Fig. 2). By the year 2012, the species was virtually extinct in European Russia, western and central Siberia, and Kazakhstan; only single birds were observed in areas where it was superabundant until the mid-1990s.

A GAM that related extinction year to latitude and longitude as variables received the greatest support, and model fit was good (Table 1). Models containing land cover as variable were within 2 ΔAIC_c units, but removing the variable longitude resulted in a large increase in AIC_c, suggesting that this was the most influential variable (Table 1). A plot of the best model (holding human population fixed at the variable mean) suggested fast progressing extinction from the northwest to the southeast of the breeding range (Fig. 3). The species therefore seems to have retracted eastwards by about 5000 km in just under 25 years, which is equivalent to the breeding range receding by 200 km/year.

Extensive trapping and trade along the entire Chinese flyway continued after it was banned in 1997. Most cases of illegal trapping and consumption of the species were reported from the province of Guangdong in southern China (Fig. 1). Publicly reported annual totals of confiscated birds ranged from 400 (in 2006) to 119,000 (in 2001) (mean 25,140 [SD 30,228], $n = 14$ years) (Fig. 1 & Supporting Information). Chinese authorities and the police seized more than 2 million songbirds as recently as 2013 in a single raid (not all of them Yellow-breasted Bunting) (Fig. 4 & Supporting Information); therefore, it seems likely that the confiscated numbers we report here represent only a fraction of the illegally trapped birds. Buntings were not only trapped and confiscated in Guangdong province, where most of them are consumed, but also along the entire Chinese flyway up to 2500 km away from Guangdong (Fig. 1).

Our scenarios of potential factors that may have caused the observed population decline suggested that a harvest of 2% of the world population in 1980 and a subsequent gradual increase of 0.2% per year to 8.6% in 2013 would cause a population decline similar to the decline estimated from the monitoring population data (mean annual population growth rate $\lambda = 0.92$) (Fig. 5). A decrease in carrying capacity, simulating a deterioration or loss of habitat, produced much less severe declines than observed. Increasing both adult and first year mortality in our environmental pollution scenario led to population declines of a magnitude similar to the observed declines. However, an increase in mortality of >10% (mean $\lambda = 0.90$) was necessary to produce a decline consistent with the actual data (Fig. 5). The scenario combining lower

Table 1. Generalized additive models explaining variation in the year of extinction of local Yellow-breasted Bunting populations.[a]

Model no.	*Intercept*	*Long.*	*Lat.*	*Land cover*	*Human population density*	*AIC_c[b]*	*ΔAIC_c[c]*	*w_i[d]*	*Adjusted R^2*	*Deviance explained (%)*
1	2003	+	+		0.0011	445.90	0.00	0.42	0.46	49.60
2	2006	+	+	+	−0.0010	446.90	1.00	0.26	0.50	53.70
3	2005	+		+	−0.0022	447.50	1.62	0.19	0.46	49.00
4	2003	+			0.0000	448.20	2.30	0.13	0.43	44.60
5	2009		+	+	0.0022	471.50	25.65	0.00	0.22	25.50
6	2003		+		0.0070	473.20	27.28	0.00	0.20	23.00

[a]*A plus sign indicates the variable was included in the model.*
[b]*Akaike's information criterion adjusted for small sample size.*
[c]*AICc difference to best model.*
[d]*Akaike weight.*

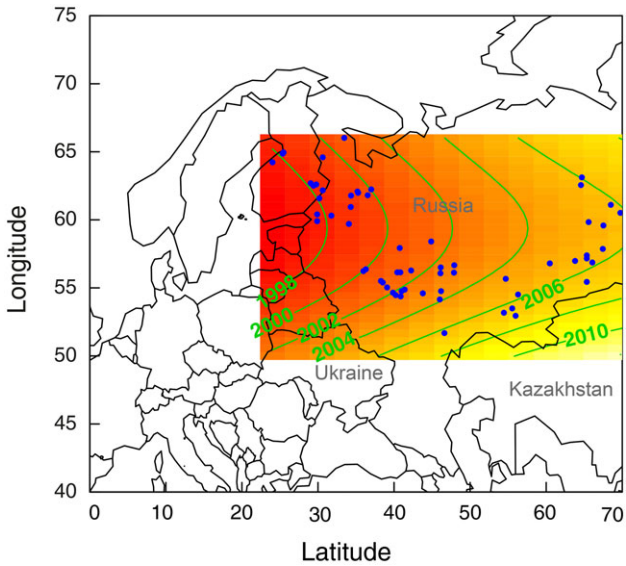

Figure 3. Modeled Yellow-breasted Bunting extinction time across the western and central parts of its range as a function of latitude and longitude (generalized additive model). Human population density was included as covariate and held fixed in the plot at the variable mean (dots, sites from which data on the year of extinction were used to parameterize the model). Contour lines separate areas of similar predicted extinction time, more intense shading corresponds to earlier extinction.

Figure 4. Yellow-breasted Buntings from a charge of 1600 that were confiscated at a trapping site (Foshan, Guangdong province, China, 1 November 2012). Photo by Huang Qiusheng.

survival and decreased carrying capacity differed only marginally from the scenario that contained a mortality increase alone and required a similarly large increase in mortality of >10% to be consistent with the observed population decline (Fig. 5).

Discussion

We found that the world population of the formerly superabundant Yellow-Breasted Bunting has collapsed during the past 25 years and that the range of the species retracted eastward by 5000 km. Our results suggest that trapping of the species in China did not cease when it was banned in 1997; rather, it continued at very high levels.

Simulated population trajectories indicated that the observed decline could have been caused by an initial harvest of 2% of the population and an increase of 0.2% annually to a harvested proportion of 8.6% in 2013. Assuming a population size of 100 million birds (a guess based on range size and large-scale estimates of population densities of 1 singing male/ha in the core breeding areas) during the 1980s, the harvest in 1980 and 2013 would have needed to be approximately 2 million birds and 8.6 million birds, respectively. These orders of magnitude seem realistic based on reported confiscation numbers, suggesting that extensive trapping along the flyway, and perhaps also in wintering areas, could have caused, or at least strongly contributed to, the observed decline.

Yellow-breasted Buntings from the entire breeding range fly along the eastern Chinese coast on their way to the wintering areas and therefore have to pass the described bottleneck of extremely high trapping pressure. The demand, trade, and consumption of all wildlife

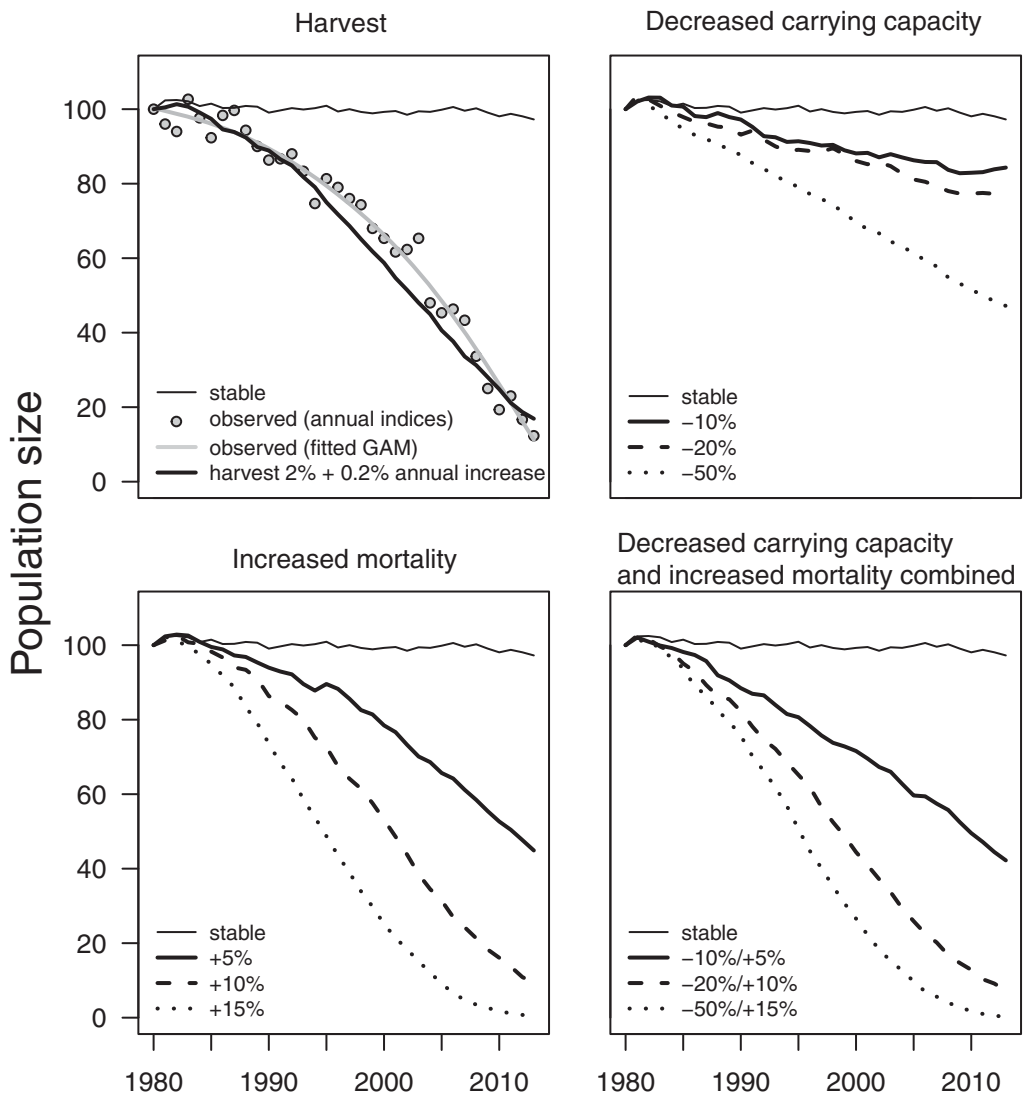

Figure 5. Simulated population size of Yellow-breasted Bunting over 34 years based on 4 scenarios affecting demographic parameters (lines, mean estimated population trajectory for 100 simulations of a population model run in Vortex). Estimates of life history traits used in the model and input model parameters are in Supporting Information. In the plot of the harvest scenario, fitted values from the observed trend and the generalized additive model (GAM) smoother function (Fig. 2) are shown for comparison.

across the flyway of the Yellow-breasted Bunting increased drastically over the last decade (Lau et al. 1996). The main reason for this trend is a general increase in living standards as mirrored by a massive increase in gross domestic product in China (Lau et al. 1996). Sixty percent of the Chinese human population consumes wildlife, and the main consumer group is young men with high educational status and incomes (Zhang et al. 2008). From 1992 to 1997, more than 10,000 (mostly Chinese) tourists visited Sanshui city (Guangdong province, China) for an annual food festival, where several hundred thousand Yellow-breasted Buntings were consumed (Chan 2004) (Supporting Information), and consumption of Yellow-breasted Buntings continued after trapping was outlawed in 1997. Yellow-breasted Buntings and other birds are not consumed to meet the basic nutritional requirements of an increasing (and mostly poor) human population; rather, they have become a fancy dish among comparatively wealthy people (Liang et al. 2013).

Bird hunting used to be carried out for subsistence until the 1980s, but recently entire villages have been living on bird trapping and sell large numbers of various species to dealers, who travel the countryside (Liang et al. 2013). Prices of wild-caught animals are rising quickly (Lau et al. 1996). A Yellow-breasted Bunting is currently sold for approximately $US8–11/bird, and locally prices of $US30–40 have been reported (Supporting Information). The growing prosperity of the Chinese means more

people can afford to buy wildlife, despite rising prices (Liang et al. 2013). Furthermore, improved infrastructure allows transport of sought-after wildlife over large distances (Lau et al. 1996; Sodhi et al. 2004).

A further increase in demand results from the recent opening of borders between China and neighboring states (e.g., Vietnam, Indonesia, Laos), which boosted wildlife trade (35 million individuals of CITES-listed species in 1998–2007 [Lau et al. 1996; Nijman 2010]). Overexploitation and consumption are now seen as the most important single driver of species endangerment and extinction in China; 53.5% of endangered bird species are threatened by harvesting for food (Yiming & Wilcove 2005). We therefore conclude that high and possibly intensifying harvest, even after its ban, has played an important role in the rapid collapse of the global Yellow-breasted Bunting population.

Large-scale land-use changes may be contributing to the population collapse. On the breeding grounds, such changes were observed after the breakup of the Soviet Union in 1991, namely the abandonment of more than 30 million ha of arable land (Schierhorn et al. 2013) and a sharp decline in livestock populations (Dubinin et al. 2011). This change resulted in spontaneous vegetation succession on former cropland, hay meadows, and pastures over vast areas (Dubinin et al. 2011). However, the Yellow-breasted Bunting is a species of early successional stages (Glutz von Blotzheim & Bauer 1997); therefore, habitat availability is likely to have increased on the breeding grounds since 1991. We detected no initial increase in population size after 1991. Our population model suggested that decreased carrying capacity is unlikely to explain the population collapse, even if 50% of the available habitat were lost. We therefore consider it unlikely that habitat loss was the key driver of the decline.

Rapid population collapses can also be caused by disease or environmental pollution. Our population model suggested that an annual increase of adult and first year bunting mortality of at least 10% would have been necessary for the population to decline as rapidly as it did. It is possible that such mortality could have been caused by environmental pollution, as has been described for other bird species with very large populations that collapsed within a few years (e.g., *Gyps* vultures [Green et al. 2004]). In China, where the most important stopover sites of the Yellow-breasted Bunting are situated, pesticide use in agriculture more than doubled between 1990 (740,000 t) and 2012 (1,620,000 t [Zhang et al. 2011]). Agricultural intensification has also been observed on the wintering grounds of the species in Vietnam and Thailand, namely in rice systems. Pesticides can affect bird populations directly (e.g., via acute mortality, sublethal stress, reduced fertility [Fry 1995]) or indirectly through a reduction of invertebrate food abundance (e.g., Hallmann et al. 2014). However, we are not aware of any reported acute mortality events that would have killed millions of songbirds on flyway stopover sites or wintering grounds.

Our habitat loss scenario in the population models, while exploring rather extreme values in the extent of lost habitat, indicated that habitat loss alone could not have caused the observed population decline. We could not determine whether increases in mortality were solely due to unsustainable harvest, increasing environmental pollution, or a combination of these factors. However, the levels of harvest necessary to cause the observed population collapse seem realistic in the light of publicly available confiscation numbers. The combined evidence suggests that songbird trapping levels in China are currently unsustainable and that trapping at least partly contributed to the decline. There are numerous, but relatively uncommon or range-restricted species whose populations declined rapidly due to increasing trade or consumption in Asia (van Balen et al. 2000; Liu & Weng 2014). However, a collapse in such an extraordinarily populous species as the Yellow-breasted Bunting, whose range stretched over an entire continent, is similar in extent to the demise of the Passenger Pigeon. The Passenger Pigeon is commonly considered to have been the most numerous bird in the world in the early 1800s (estimated 3 billion birds), but it went extinct in 1914 after decades of industrial-scale hunting (Schorger 1973). As described here for Yellow-breasted Bunting, pigeon numbers collapsed in a period of fast human population and economic growth and increasing human mobility along the migration routes (Schorger 1973).

There is preliminary evidence that other abundant songbird species with large ranges might decline due to trapping in East Asia. Dale and Hansen (2013) report population collapses in Rustic Bunting (*Emberiza rustica*) across Scandinavia, a species closely related to the Yellow-breasted Bunting. A long-term study at Lake Baikal, Siberia, revealed significant and strong declines between 1984 and 2007 in 5 *Emberiza* species and generally more negative population trends in long-distance than in short-distance and resident birds (Ananin 2011). All of the aforementioned bunting species have similar migration routes and wintering areas and are trapped in China as well (Supporting Information). They are less conspicuous and less gregarious at roosts than Yellow-breasted Bunting and do not occur at equally high local densities on the breeding grounds. Therefore, they are probably less well recorded and declines remain undetected in many areas.

Little is known about population trends, environmental threats, and persecution pressure of common and widespread taxa in Asia (Yong et al. 2015). There is an urgent need to strengthen biodiversity monitoring efforts in the eastern Palearctic. The steeply declining abundance of the Yellow-breasted Bunting provides a recent example of how human persecution can contribute to population collapses of widespread and superabundant

species. Birds have important ecosystem functions (Şekercioğlu et al. 2004), such as pest control in insectivorous species like the Yellow-breasted Bunting. These ecosystem services might be disrupted if precipitous declines of abundant species continue or accelerate in the near future, with potentially profound and direct implications for society.

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Supporting Information

Information on the sites from which long-term monitoring data for Yellow-breasted Bunting were available; categories used to classify qualitative trend information for Yellow-breasted Bunting plotted in Fig. 1; incidents of illegal trapping Yellow-breasted Buntings in China; and demographic and habitat parameters used in VORTEX population models (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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