Global Ecology and Conservation 4 (2015) 137–145

Contents lists available at ScienceDirect

Global Ecology and Conservation

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

Original research article

Human harvest, climate change and their synergistic effects drove the Chinese Crested Tern to the brink of extinction

Shuihua Chen[a,*], Zhongyong Fan[a], Daniel D. Roby[b], Yiwei Lu[a], Cangsong Chen[a], Qin Huang[a], Lijing Cheng[c], Jiang Zhu[c]

[a] *Department of Life Science, Zhejiang Museum of Natural History, Hangzhou, 310014, China*

[b] *U.S. Geological Survey-Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA*

[c] *Institute of Atmospheric Physics, Chinese Academy of Sciences, Beijing, 100029, China*

ARTICLE INFO

Article history:
Received 24 June 2015
Accepted 26 June 2015
Available online 3 July 2015

Keywords:
Synergistic effect
Species endangerment
Human harvest
Climate change
Chinese Crested Tern

ABSTRACT

Synergistic effect refers to simultaneous actions of separate factors which have a greater total effect than the sum of the individual factor effects. However, there has been a limited knowledge on how synergistic effects occur and individual roles of different drivers are not often considered. Therefore, it becomes quite challenging to manage multiple threatening processes simultaneously in order to mitigate biodiversity loss. In this regard, our hypothesis is, if the traits actually play different roles in the synergistic interaction, conservation efforts could be made more effectively. To understand the synergistic effect and test our hypothesis, we examined the processes associated with the endangerment of critically endangered Chinese Crested Tern (*Thalasseus bernsteini*), whose total population number was estimated no more than 50. Through monitoring of breeding colonies and investigations into causative factors, combined with other data on human activities, we found that widespread human harvest of seabird eggs and increasing frequency of typhoons are the major factors that threatened the Chinese Crested Tern. Furthermore, 28 percent of breeding failures were due to the synergistic effects in which egg harvest-induced renestings suffered the higher frequent typhoons. In such combined interactions, the egg harvest has clearly served as a proximal factor for the population decline, and the superimposition of enhanced typhoon activity further accelerated the species toward imminent extinction. Our findings suggest that species endangerment, on one hand, should be treated as a synergistic process, while conservation efforts, on the other hand, should focus principally on combatting the threat that triggers synergistic effects.

1. Introduction

Species go extinct when they are no longer able to survive under changing environmental conditions or against superior competition from other species. So far, research on extinction has focused on why extinct species were prone to extinction (intrinsic biological traits) and what drove them to extinction (extrinsic threats). Intrinsic biological traits might include rarity (Simberloff, 1986; Duncan and Young, 2000; Davies et al., 2000), habitat specialization (Frank and Amarasekare, 1998;

---

[*] Correspondence to: Zhejiang Museum of Natural History, 6 Westlake Cultural Square, Hangzhou, 310014, China. Tel.: +86 571 88212787 (office), 86 13957136429 (mob).

E-mail address: chensh@zmnh.com (S. Chen).

http://dx.doi.org/10.1016/j.gecco.2015.06.006

Owens and Bennett, 2000), trophic level (Holt et al., 1999; Holyoak, 2000), and body size (Burbidge and McKenzie, 1989; Blackburn and Gaston, 1997; Cardillo et al., 2005). Species declines and extinctions have been attributed to a number of extrinsic threats, including habitat destruction and fragmentation (Mace and Balmford, 2000), overexploitation (Price and Gittleman, 2007), local environmental stochasticity (Purvis et al., 2000; Pimm et al., 2006), climate change (Thomas et al., 2004; Sekercioglu et al., 2008), and invasive species (Wilcove et al., 1998; Fritts and Rodda, 1998), but rarely is the cause or causes of extinction clearly understood. Extinction research has been successful in providing some broad generalities that mostly derive from fossil and meta-analytic studies (Diamond, 1989; Raup, 1994; Purvis et al., 2000), but these studies have both limitations and difficulties in discerning exactly what factors were responsible for extinction (Brook et al., 2008). In addition to the "why" and "what" of extinction, it is also important to understand the "how" in conservation biology—how drivers of extinction work. Answering the "how" question is usually dependent on empirical studies, but is crucial for effective conservation and efficient restoration through prioritization of efforts to recover threatened taxa.

Recent researches suggested that different traits usually act jointly to promote extinction risk. For example, deforestation inevitably causes fragmentation, which in turn leads to protracted loss of long-lived taxa, such as tropical trees (Brook et al., 2003); interactions between natural abundance and degree of specialization led to a greater reduction in the growth rates of rare and specialized beetle species in fragments than the sum total of their growth-rate reductions in continuous forests (Davies et al., 2004); an interaction between global warming and disease resulted in the disappearance of 40% of 50 endemic frog and toad species from the highland forests of Costa Rica (Pounds et al., 2006). Overkill, habitat destruction, introduced species and chains of extinction were regarded as the evil-quartet for driving human-caused extinction (Diamond, 1989), and most extinctions might involve an interaction between these factors (Koh et al., 2004; Mora et al., 2007). The role of synergistic effect was suggested for describing simultaneous actions of separate factors (intrinsic biological traits or extrinsic threats) that have a greater total effect on threatened species than the sum of their individual factor effects (Davies et al., 2004; Brook et al., 2008). The implication of synergy model is that by treating extinction as a synergistic process the predictions of risk for most species can approximate reality, and therefore, conservation efforts can be made more effective (Fagan and Holmes, 2006; Malcolm et al., 2006).

However, the synergy model also introduces a big challenge that the policy to mitigate biodiversity loss must accept the need to manage multiple threatening processes simultaneously over longer terms (Brook et al., 2008). This is true if one does not know how the traits interact. We thus hypothesized that, if these traits actually played different roles in the interaction, such as one is active and the other is passive, conservation efforts could focus just on the active process and eliminate the threat of synergistic effect, thereby managing only one threatening factor, instead of multiple ones simultaneously. However, there has been limited understanding so far on how synergistic effects occur and the individual roles of different traits/drivers in the interaction have not been considered. To understand the synergistic effect and test our hypothesis, we examined the 10 year monitoring data of the critically endangered Chinese Crested Tern (*Thalasseus bernsteini*), and combined the data of egg harvest, typhoon and fishing activities, in attempt to detect the factors that led to the endangerment of this species. We also aimed to test whether there is any synergistic effect between the factors or not, and if such effect existed at all, how it happened and the roles of different drivers in the interaction.

2. Methods

2.1. Study species and area

The Chinese Crested Tern has long been a poorly known seabird breeding at remote islands off the southeast coast of China (Collar et al., 2001). The species was considered extinct for 63 years before two small breeding colonies were discovered in the Mazu Archipelago off the Fujian coast and in the Jiushan Archipelago off the Zhejiang coast in 2000 and 2004, respectively (Liang et al., 2000; Chen et al., 2005). The colony in the Jiushan Islands moved to the Wuzhishan Archipelago, about 100 km away, in 2008 (Chen et al., 2005). The total population of Chinese Crested Terns has been estimated at no more than 50 individuals, and the species was and remains categorized as Critically Endangered on the IUCN Red List (Chen et al., 2009; BirdLife International, 2015; IUCN, 2015).

To explore the factors leading to this species' endangerment, we closely monitored the breeding colonies at the Jiushan Archipelago and the Wuzhishan Archipelago in Zhejiang from 2004 to 2013, especially numbers of breeding individuals, breeding success, and the factors limiting colony size and nesting success. In addition, based on the results of previous monitoring, we treated egg harvest and typhoon as two major potential threats, and investigated the status of seabird egg harvest along the coast of Zhejiang Province, and collected data on typhoons impacting the coast of Zhejiang and Fujian Province from 1950 to 2012.

The Zhejiang continental coastline stretches over 2200 km (Fig. 1), from about 27°06′N to 31°11′N, connecting Fujian coast in the south, and facing the East China sea and Taiwan Strait in the east. Of all the islands off the coast of Zhejiang Province, 2886 are uninhabited islands, or 94.3% of the total. Of these, 1383 islands (48%) are situated off the northern coastline of Zhejiang Province, forming the Zhoushan Group. We monitored the breeding colonies of the Chinese Crested Terns in the Jiushan and Wuzhishan archipelago. The Jiushan Archipelago (122°10′E, 29°26′N) is situated 19 km off the coast of Xiangshan County, eastern Zhejiang Province. The Wuzhishan Archipelago (121°50′E, 30°13′N) is located at the mouth of Hangzhou Bay, 7 km offshore of the biggest island of Zhoushan Group.

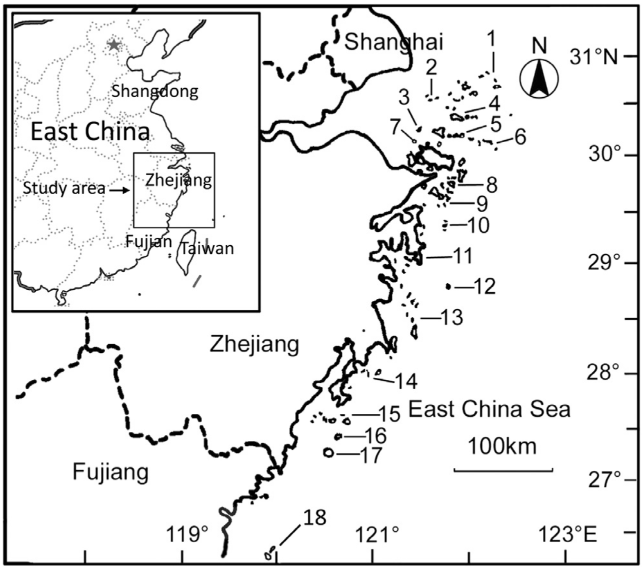

Fig. 1. Coast of Zhejiang Province, P.R. China, showing the two island groups where nesting Chinese Crested Terns were monitored (7, 10) and the 17 island groups where harvest of seabird eggs was investigated (1–17). 1-Shengsi; 2-Qiqu; 3-Huoshan; 4-Qushan; 5-Changtu; 6-Zhongjieshan; 7-Wuzhishan; 8-Putuo; 9-Meisan; 10-Jiushan; 11-Nantian; 12-Yushan; 13-Taizhou; 14-Luxi; 15-Dongtou; 16-Beiji; 17-Nanji; 18-Mazu.

2.2. *Monitoring of nest success*

From 2004 to 2007, we closely monitored the mixed colony of Greater Crested Terns (*Thalasseus bergii*) and Chinese Crested Terns in the Jiushan Islands, where Chinese Crested Terns were first discovered nesting off the coast of Zhejiang in 2004. We continued monitoring nesting attempts by Chinese Crested Tern at the Wuzhishan Islands from 2008 to 2013, after the tern colony suffered a complete breeding failure due to egg harvest and shifted there from the Jiushan Islands (Chen et al., 2010). During the breeding season from mid-May to the end of September, we usually visited the breeding colonies by boat every other day. As the Chinese Crested Terns usually nest among a big colony of the Greater Crested Terns on the edge ground of an island, and have distinct plumage from the latter, we observed nesting birds using 8–10× binoculars from boats and then took photos with digital SLR cameras equipped with 200–300 mm telephoto lens to count the number of active nests and determine the breeding status of each Chinese Crested Tern present. If we could not determine the breeding status of a Chinese Crested Tern from the boat, we would land on the nesting island to have a closer look. During monitoring, we focused on (1) determining the number of Chinese Crested Terns present, (2) the breeding status of each Chinese Crested Tern present, the fate of each nesting attempt by Chinese Crested Terns, and, if the nesting attempt failed, the cause of nest failure.

2.3. *Investigation of illegal egg harvest*

From 2003 to 2006, we conducted surveys of seabird breeding colonies and investigated the incidence of poaching of seabird eggs along the Zhejiang coast. In total, we surveyed 2740 islands, comprising 95% of the uninhabited islands and reefs along the Zhejiang coast, and including: Shengsi Archipelago, Qiqu Archipelago, Huoshan Archipelago, Qushan and adjacent islands, Wuzhishan Archipelago, Zhongjieshan Archipelago, Changtu Archipelago, Putuo and adjacent islands, Jiushan Archipelago, Meisan Archipelago, Yushan Archipelago, Nantian and adjacent islands, Taizhou Archipelago, Luxi and adjacent islands, Dongtou Archipelago, Beiji Archipelago, and Nanji Archipelago. During each survey, we usually hired fishing boats to transport the survey team to the islands. Once a seabird breeding colony was detected on an island, we would observe with binoculars and take photographs to identify the breeding species present and estimate the numbers of each. We landed on each breeding island to confirm whether harvest of seabird eggs had occurred. There were no big mammals besides rats on these islands, and rats and raptors usually would not cause many nests empty or missing, thus we judged a breeding colony as having been egged based on the following criteria: (1) direct encounters with egg harvesters, (2) eggs removed from nests and left on the island, (3) presence of many empty nests that did not contain eggs or chicks, for those seabird species that build obvious nest structures (Black-tailed Gull [*Larus crassirostris*], Bridled Tern [*Onychoprion anaethetus*], Roseate Tern [*Sterna dougallii*]), (4) no eggs present at least two weeks after egg-laying normally is initiated (1 May for Black-tailed Gulls, 1 June for all tern species), (5) no eggs or chicks present on a colony when the colony should have been late in the breeding cycle, (6) nesting chronology delayed by about one month compared to normal, and (7) less than half the number of seabird eggs or chicks present.

During each survey, we would interview local fishermen, marine bureau officials, and nature reserve administrative staff by asking the following questions: (1) who were the potential egg harvesters, (2) for what purpose had the eggs been collected, for the harvesters' own consumption or for subsequent sale, and (3) if the eggs had been harvested with the intent to sell, who was the intended purchaser. A total of 32 interviews with definite answers to the three questions were obtained.

2.4. *Fishing activity data collection and analysis*

To estimate the potential impacts of fishing activities on egg harvest, we collected data on fishing activity along the coast of Zhejiang Province during 1950–1992 from the *Zhejiang Provincial Journal of Fishery* (Compilation Committee of the Zhejiang Provincial Journal of Fishery, 1999), and during 1993–2013 from the *China Fisheries Yearbook 1993–2013* (Fishery Bureau of the People's Republic of China, 1993–2013). Level of fishing activity was indicated by numbers of fishing boats (wooden junks, motorized vessels, and total fishing vessels), number of people engaged in fisheries, and fish catches. We analyzed and tested for trends in fishing activity level during the period 1950–2013 using Linear Regression analysis.

2.5. *Typhoon data collection and analysis*

We obtained the data of typhoons from the Unisys Weather best track dataset (http://weather.unisys.com/hurricane/index.php) which provides the data of all typhoons that impacted the coast of Zhejiang and Fujian provinces during 1950–2012. Seven categories of tropical cyclones were considered in this study, based on definitions from the Saffir–Simpson Scale. The seven categories included, in order of increasing intensity: Tropical Depression, Tropical Storm, and Hurricane Level 1 to 5. In order to identify typhoons that had impacted the Zhejiang and Fujian coastal area, we adopted the following criteria: (1) the locations of the coastlines of Zhejiang and Fujian were identified with a spatial resolution of 1°, and (2) if the center of a typhoon was within 300 km (influence radius) of the Zhejiang and Fujian coastline, we assumed that this typhoon would impact the coastline of Zhejiang and Fujian provinces. An influence radius of 300 km was chosen because the diameter of a storm varies among storms, with a minimum influence radius of less than 100 km and a maximum of 1000 km, so 300 km was a reasonable approximation for the averaged size (diameter) of a tropical cyclone. Observational studies have indicated that tropical cyclones can have impacts on ocean conditions at least 300 km from the storm center as a global average (Mei et al., 2013; Cheng et al., 2014). We obtained data on a total of 532 typhoons and analyzed the following data for each typhoon: sequence number (assigned number in the typhoon season), date of impact (the date when the typhoon was closest to the Zhejiang or Fujian coastline), and storm intensity or category. Based on these data, we analyzed and tested for trends in typhoon impact date, typhoon frequency (number/year), and average typhoon intensity during the period from 1950 to 2012 using Linear Regression analysis.

3. Results

3.1. *Nest failures and their causes*

During the 10 breeding seasons of our study, we monitored a total of 45 nesting attempts by Chinese Crested Terns (including 12 re-nesting attempts after the first nesting attempt of the breeding season failed). Of this sample, 25 nests (55.6%) failed. Egg harvest by local fishermen and typhoons were the two major causes of nest failure, accounting for 44% ($n = 11$ nests) and 48% ($n = 12$ nests) of failed nests, respectively. The causes of the other two nest failures (8%) were unknown. Most of the failures ($n = 18$, 72%) occurred before 2008; since then the two breeding colonies have been well protected from egg harvest.

3.2. *Illegal egg harvest*

We monitored a total of 49 seabird breeding colonies, including those of Black-tailed Gulls, Roseate Terns, Black-naped Terns (*Sterna sumatrana*), Bridled Terns, Greater Crested Terns, and Chinese Crested Terns. We found that 43 colonies (87.8%) suffered egg harvest, indicating that egg harvest was widespread along this section of coastline, especially at seabird breeding islands that were unguarded. Our interviews with local fishermen and administrative staff for marine and nature reserves indicated that seabird eggs were collected mainly by fishermen during their fishing activities (81%) and sold to tourists for consumption at local restaurants (72%).

3.3. *Fishing activities and tourism*

Before 1950 wooden sailing junks were the only fishing boats used, but after 1950 their numbers declined dramatically ($r^2 = 0.917$, $P < 0.001$) as junks were replaced by motorized vessels (Table 1). By the early 1980s, motorized vessels replaced wooden junks as the predominant type of fishing boat and increased significantly in number since then ($r^2 = 0.748$, $P < 0.001$), while the overall number of fishing boats increased significantly from 1950 to 2013 ($r^2 = 0.270$, $P < 0.001$). Numbers of fishers and fishery catches also showed significant increases ($r^2 = 0.434$, $P < 0.001$; $r^2 = 0.789$, $P < 0.001$)

Table 1
Trends of coastal fisheries in Zhejiang province from 1950 to 2013.

	Sample size	r^2	Slope	t
Wooden junk	42	0.897	−561.7	−20.985*
Motorized vessel	40	0.748	689.7	10.748*
Total vessel	42	0.270	164.6	3.851*
Fishery catches	62	0.789	5.402	14.979*
Number of fishers	44	0.434	1531.4	5.675*

The correlations were tested with Linear Regression.

* $p < 0.001$.

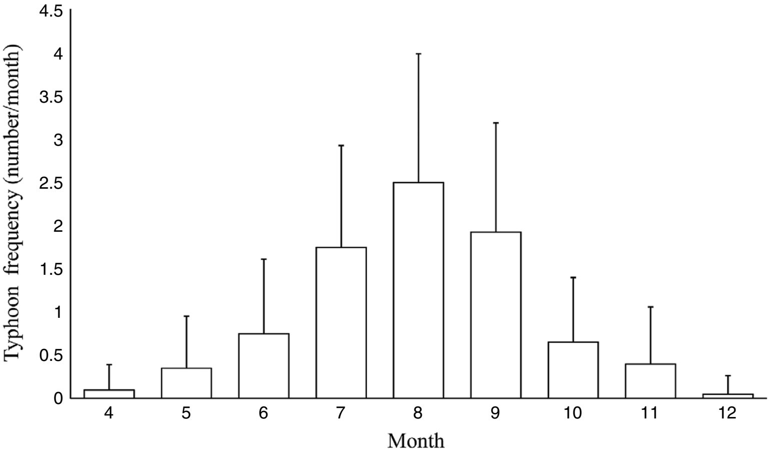

Fig. 2. The typhoon frequency and time impacting the coast of Zhejiang and Fujian provinces.

since 1950. Concurrently, the numbers of tourists in Zhejiang, as an indicator of the potential consumer market for seabird eggs, has also increased rapidly in recent decades (Tourism Bureau of Zhejiang Province, 2013). Thus increasing fishing activity and tourism likely combined to exacerbate the intensity of egg harvest at seabird breeding colonies along the Zhejiang coast, including those of the Chinese Crested Tern.

3.4. Typhoon occurrence

A total of 532 typhoons were recorded in this region during the 63-year study period, occurring from April to December, with a peak (2.49 typhoons/month) of occurrence in August (Fig. 2). We further analyzed these data to detect changes in the impact date, frequency, and intensity of typhoons from 1953 to 2012. The results indicated that, while there was no significant change in typhoon impact date ($r^2 < 0.0005$, $P = 0.877$) from 1950 to 2012, average typhoon intensity decreased slightly but significantly ($r^2 = 0.010$, $P = 0.019$), and typhoon frequency increased significantly ($r^2 = 0.112$, $p = 0.007$) during the study period (Fig. 3). Although the average intensity of typhoons decreased during the study period, the increasing frequency of typhoons likely caused higher rates of nest failure for seabirds nesting on exposed coastal islands, including Chinese Crested Terns.

3.5. Synergistic effects

Seven of 12 nesting attempts that failed due to typhoons (58%) were renesting attempts following the failure of the first nesting attempt because of egg harvest. In the absence of egg harvest, typhoon-induced nest failures would have declined from 12 to five. These seven nesting failures resulted from the synergistic interaction between egg harvest and typhoons (Fig. 4). A conceptual model of how egg harvest and typhoons had a synergistic effect on tern nest success is depicted in Fig. 5. Normally, Chinese Crested Terns initiate egg-laying in early June and, with a ca. 25-day incubation period and a ca. 33-day chick-rearing period, successful reproduction can be completed by early August (Chen et al., 2011). If egg harvest occurs, however, as we recorded on several occasions, renesting usually commences by early July and, consequently, would then not be completed until early September. Due to this delay in nest initiation, the tern breeding cycle overlaps completely with the season of peak typhoon occurrence, causing higher nest failure rates than would otherwise be expected. This increment in nest failure rate is the synergistic effect generated by both egg harvest and typhoons combined. The typhoon frequencies during early breeding season are relatively lower (0.746/month in June and 1.746/month in July), plus the long coastline of Zhejiang and Fujian provinces (5500 km, from about 23°39′N to 31°11′N), thus in the absence of egg harvest, Chinese Crested Terns would likely complete the breeding cycle and depart the breeding colony before the period of highest risk

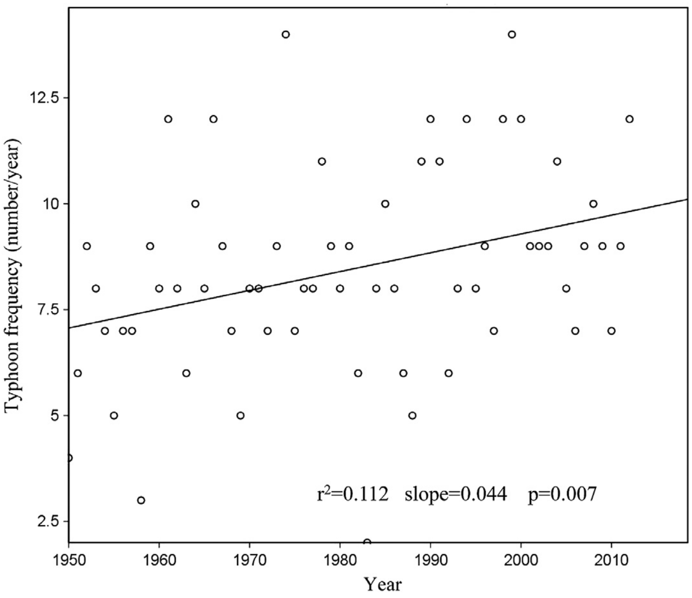

Fig. 3. Dynamics of typhoon frequency (number/year) impacting the coast of Zhejiang and Fujian provinces from 1950 to 2012.

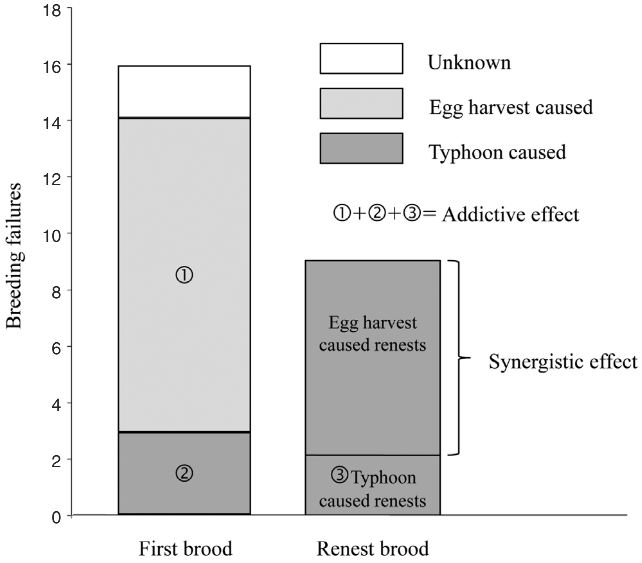

Fig. 4. Number of failed nesting attempts by Chinese Crested Terns and their causes at breeding colonies in Zhejiang Province from 2000 to 2013. Dark gray area indicates nesting attempts that failed to typhoons, light gray area indicates nesting attempts that failed due to egg harvest, and blank area indicated nesting attempts that failed due to unknown causes. Egg harvest caused breeding pairs to renest, nesting attempts that subsequently failed due to typhoons, producing a synergistic effect between egg harvest and typhoons.

from typhoons, and in the absence of typhoons the reproductive output from renesting attempts would compensate for nest failures caused by egg harvest.

4. Discussion

4.1. Human harvest, climate change and their synergistic effects drove the Chinese Crested Tern to the brink of extinction

Each species exists within an ecological niche, which includes all of the environmental factors within its habitats. These factors not only define the living space for the species, but also act as constraints, limiting its population size and distribution (Wiens and Graham, 2005; Pearman et al., 2007). If one or more limiting factors change, their relationships with other limiting factors also change accordingly, resulting in niche expansion or contraction. For reproduction, a species needs not

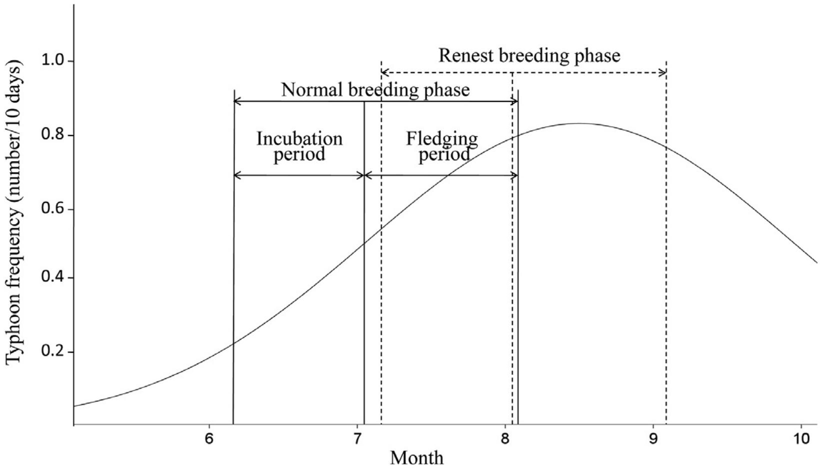

Fig. 5. Diagram showing how the synergistic effect forms. *X* axis indicates the breeding period from June (6) to September (9), *Y* axis indicates the number of typhoons that occurred per 10-day period during one breeding season, such as 1–10 June, 11–20 June, 21–30 June, and so on. The curved line represents the smoothed relative frequency of typhoons across the season.

only suitable habitat, but also suitable time span. This time span can be treated as a niche in time direction for this species. Most seabirds breeding in islands and with open nests are usually more sensitive to seasonal change due to the weather and food availability (Schreiber and Burger, 2002). Thus, it is crucial for seabirds to complete their breeding cycles within the suitable time span. For the Chinese Crested Terns, early June to late September is their breeding time niche, and the time length of about two months for the species to complete the breeding cycle is its fundamental niche. Nevertheless, the typhoons occurring frequently in summer shorten its breeding time niche, and egg harvests lead to the niche's further contraction. When the time left was not enough for them to complete their breeding cycle, their population began to collapse. The breeding colonies still extant in Zhejiang and Mazu are probably the remnant populations filtered by egg harvests and typhoons.

Human harvest, climate change, and their synergistic effects are likely not the entire explanation for why the Chinese Crested Tern is so close to extinction. Five other species of seabirds, including one gull and four terns, breed in the same region used by Chinese Crested Terns. With the exception of the black-tailed gull, which initiates breeding about a month earlier, the other four species are terns that have almost the same reproductive chronology as Chinese Crested Terns (Yan et al., 2006; Fan et al., 2011), including the Greater Crested Tern with which Chinese Crested Terns invariably nest (Chen et al., 2011). Consequently, Greater Crested Terns nesting along the coast of Zhejiang Province are likely to have experienced the same challenges as Chinese Crested Terns. Why, then, is the Chinese Crested Tern the only critically endangered species among them? Historically, Chinese Crested Terns nested along the east coast of China from Shandong to Fujian provinces, but now they are only found in Zhejiang and Fujian provinces (Chen et al., 2009). In comparison with four other sympatric tern species, the Chinese Crested Tern is the only species whose historical breeding range was confined to the east China coast (Yan et al., 2006; del Hoyo et al., 1996). The human harvest and climate change that we have documented surely had similar impacts on all populations of marine terns breeding in this area; however, local human harvest and weather events would have led to only local extinctions for the four more widespread species of terns. Breeding populations of these widespread tern species could persist in the region in the face of human harvest and climate change because of the influx of individuals from other source populations, whereas in the case of the Chinese Crested Tern no source populations existed.

In June and July of 1937, 21 specimens of the Chinese Crested Tern were collected from a single-species breeding colony off the coast of Shandong (Shaw, 1938), suggesting that the population of Chinese Crested Terns was likely larger at that time. Sixty-three years later, when the species was rediscovered in 2000, it had reached the brink of extinction. We cannot be certain which factors resulted in the original population decline of this species, including habitat destruction, overexploitation, marine pollution, egg harvest, climate change, narrow ecological niche, or even natural rarity (Davies et al., 2004; Brook et al., 2008; Chen et al., 2009; Liu et al., 2009). They, even including some synergistic effects among them we have not detected, might all have ever contributed to the endangerment of the Chinese Crested Tern, but our results suggested that, for the past half-century, human harvest, climate change, and their synergistic effects played crucial roles in driving the Chinese Crested Tern to the brink of extinction.

4.2. *The roles of different drivers in the synergistic effect*

During a long history, the coast of China has been an area of military tensions because of an extended series of consecutive wars. Since 1950, when the People's Republic of China was founded, the economy along the coastline of China began to recover. With motorized vessels replacing wooden sailing junks as the major means of marine transportation and commerce, the economy of China developed rapidly, especially along the east coast of China. Recent decades have witnessed a tremendous resurgence of fisheries, as well as tourism, which together certainly brought huge pressures on populations of breeding seabirds in the region. Our findings also showed that these two factors made different contributions to synergistic effects. As egg harvest was more tightly controlled after 2008, the synergistic effects were largely eliminated. This suggests that egg harvest was the ultimate factor behind the synergistic effects of human harvest and climate change.

Typhoons are natural weather events that have persisted in the East China Sea over evolutionary time scales, and are a limiting factor that Chinese Crested Terns have had to adapt to since the species colonized the area. In the absence of egg harvest, typhoons would likely not constitute a major threat for this species, even if the frequency of typhoons increased, as it has in recent decades. As the mechanism under the endangerment of the Chinese Crested Tern is still not clear, the future conservation plan should also rely on the information from population viability analysis, genetic diversity analysis, and migration and wintering ecology. But our results imply that at this stage reducing or eliminating egg harvest is crucial for preventing the critically endangered Chinese Crested Tern from rushing toward extinction. The management actions that can achieve this goal are principally enhanced law enforcement and community education near the island groups where Chinese Crested Terns still nest.

Despite the synergistic negative effects of climate event and human harvest on the remnant population of Chinese Crested Terns, typhoons nevertheless constitute an important risk to breeding terns in the region. Typhoons occur as early as July along the southeast coast of China, and therefore can overlap with the nesting cycle of Chinese Crested Terns. Typhoons and other local risk factors that can cause nest failure or even colony abandonment, such as predators and human disturbance, dictate that a longer-term strategy for securing the future of this critically endangered species includes spreading these local risks amongst a number of breeding sites distributed across a large geographic area. As long as the entire world's population of a critically endangered species nests at just one or two separate sites, the species is vulnerable to extinction due to stochastic, catastrophic local events.

The limiting factors themselves thus become threats to endangered species whose niches have contracted. Once a species could not balance death rates with birth rates within a reduced niche space, it is ultimately doomed to extinction. Like many factors that define a species' niche, extinction is generally caused by a number of drivers that work separately or in combination. Recently, the synergistic interactions between harvest, fire, invasive species, and climate change have been revealed (Laurance et al., 2000; Malcolm et al., 2006; Carroll, 2007; Jetz et al., 2007; Mora et al., 2007). The synergistic model for species declines emphasizes the positive feedback of multiple threats via a combination of approaches, instead of focusing on the impact of a single driver or the simple additive impact of multiple drivers (Brook et al., 2008).

Human activities and climate change have been identified as the primary causes of current species extinctions (Ceballos and Ehrlich, 2002; Thomas et al., 2004; Burney and Flannery, 2005). Our finding revealed their contributions to the endangerment of the Chinese Crested Tern in an additive and even a synergistic fashion. An understanding on synergistic effects can provide insight into species endangerment and also help to make conservation plans more effectively. Synergistic effect surely makes the mechanisms of species endangerment more complicated, and thus bring a big challenge in conservation. Nevertheless, it does not mean that we have to manage multiple threatening processes simultaneously if we know the individual roles of different drivers. In most cases, human activities or human-induced traits usually act as a factor triggering other factors, even those which were previously non-threatening, natural limiting factors, thereby driving species toward extinction. The implications of our findings are that species endangerment, on one hand, should be treated as a synergistic process, while conservation efforts, on the other hand, should focus primarily on combatting the threats that trigger synergistic effects.

Acknowledgments

We are grateful to the administration of the Zhejiang Jiushan Archipelago Provincial Marine Ecological Nature Reserve and the administration of the Zhejiang Wuzhishan Archipelago Provincial Bird Nature Reserve for permission to access the breeding islands and for their assistance with monitoring, and to Fanggang Zhang, Ankang Zhang, Zhongde Wang, Xiaodong Li, Sai Wang, and Shiming Cui for their assistance with our field work. This study was funded by the National Natural Science Foundation of China (Grant No. 30570251), the Endangered Species Monitoring Fund from the State Forestry Administration of China (2010, 2013), and the Ocean Park Conservation Foundation (Hong Kong No. 4030000074). The typhoon data were downloaded from the Unisys Weather website.

References

BirdLife International, 2015. Species factsheet: *Thalasseus bernsteini*. Available online at http://www.birdlife.org (accessed January 2015).

Blackburn, T.M., Gaston, K.J., 1997. A critical assessment of the form of the interspecific relationship between abundance and body size in animals. J. Anim. Ecol. 66, 233–249.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 23, 453–460.

Brook, B.W., Sodhi, N.S., Ng, P.K., 2003. Catastrophic extinctions follow deforestation in Singapore. Nature 424, 420–423.

Burbidge, A.A., McKenzie, N.L., 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. Biol. Cons. 50, 143–198.

Burney, D.A., Flannery, T.F., 2005. Fifty millennia of catastrophic extinctions after human contact. Trends Ecol. Evol. 20, 395–401.

Cardillo, M.G., Mace, M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R., Sechrest, W., Orme, C.D., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. Science 309, 1239–1241.

Carroll, C., 2007. Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: marten and lynx in the Northern Appalachians. Conserv. Biol. 21, 1092–1104.

Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. Science 296, 904–907.

Chen, S.H., Chang, S.H., Liu, Y., Chan, S., Fan, Z.Y., Chen, C.S., Yen, C.W., Guo, D.S., 2009. Low population and severe threats: status of the Critically Endangered Chinese Crested Tern *Sterna bernsteini*. Oryx 43, 209–212.

Chen, S.H., Fan, Z.Y., Chen, C.S., Lu, Y.W., 2010. A new breeding site of the Critically Endangered Chinese Crested Tern *Sterna bernsteini* in the Wuzhishan Archipelago, eastern China. Foktail 26, 132–134.

Chen, S.H., Fan, Z.Y., Chen, C.S., Lu, Y.W., 2011. The breeding biology of Chinese crested terns in mixed species colonies in Eastern China. Bird Conserv. Int. 21, 266–273.

Chen, S.H., Yan, C.W., Fan, Z.Y., Chen, C.S., Zhang, F.G., 2005. The breeding colony of Chinese Crested Tern at Jiushan Archipelago in Zhejiang. Chin. J. Zool. 40, 96–97.

Cheng, L., Zhu, J., Sriver, R.L., 2014. Global representation of tropical cyclone-induced ocean thermal changes using Argo data – Part 1: Methods and results. Ocean Sci. Discuss. 11, 2831–2878.

Collar, N.J., Andreev, J.V., Chan, S., Crosby, M.J., 2001. Threatened Birds of Asia: The BirdLife International Red Data Book. BirdLife International, Cambridge, UK.

Compilation Committee of the Zhejiang Provincial Journal of Fishery, 1999. Zhejiang Provincial Journal of Fishery. Zhonghua Book Company, Beijing.

Davies, K.F., Margules, C.R., Lawrence, J.F., 2000. Which traits of species predict population declines in experimental forest fragments? Ecology 81, 1450–1461.

Davies, K.F., Margules, C.R., Lawrence, J.F., 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology 85, 265–271.

del Hoyo, J., Elliot, A., Sargata, J., 1996. Handbook of the Birds of the World, Vol. 3 Hoatzin to Auks. Lynx Edicions, Barcelona, Spain.

Diamond, J.M., 1989. Overviewof recent extinctions. In: Western, D., Pearl, M.C. (Eds.), Conservation for the Twenty-First Century. Oxford University Press, Oxford, UK, pp. 37–41.

Duncan, R.P., Young, J.R., 2000. Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. Ecology 81, 3048–3061.

Fagan, W.F., Holmes, E.E., 2006. Quantifying the extinction vortex. Ecol. Lett. 9, 51–60.

Fan, Z.Y., Chen, C.S., Chen, S.H., Chan, S., Lu, Y.W., 2011. Breeding seabirds along the Zhejiang coast: diversity, distribution and conservation. Chin. Birds 4, 39–45.

Fishery Bureau of the People's Republic of China, 1993–2013. China Fisheries Yearbook 1993–2013. China Agriculture Press, Beijing.

Frank, S.A., Amarasekare, P., 1998. Increasing resource specialization among competitors shifts control of diversity from local to spatial processes. Ecol. Lett. 1, 3–5.

Fritts, T.H., Rodda, G.H., 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. Ann. Rev. Ecol. Syst. 29, 113–140.

Holt, R.D., Lawton, J.H., Polis, G.A., Martinez, N.D., 1999. Trophic rank and the species–area relationship. Ecology 80, 1495–1504.

Holyoak, M., 2000. Habitat subdivision causes changes in food web structure. Ecol. Lett. 3, 509–515.

IUCN, 2015. IUCN Red List of Threatened Species. Version 2014.3. Available online at http://www.iucnredlist.org (accessed January 2015).

Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biology 5, e157.

Koh, L.P., Sodhi, N.S, Brook, B.W., 2004. Ecological correlates of extinction proneness in tropical butterflies. Conserv. Biol. 18, 1571–1578.

Laurance, W.F., Vasconcelos, H.L., Lovejoy, T.E., 2000. Forest loss and fragmentation in the Amazon: implications for wildlife conservation. Oryx 34, 39–45.

Liang, C.T., Chang, S.H., Fang, W.H., 2000. Little known oriental bird: discovery of a breeding colony of Chinese Crested Tern. Orient. Bird Club Bull. 32, 18.

Liu, Y., Guo, D.S., Qiao, Y.L., Zhang, E., Cai, B.F., 2009. Regional extirpation of critically endangered Chinese Crested Tern (*Thalasseus bernsteini*) from Shandong Coast, China? Waterbirds 42, 597–599.

Mace, G.M., Balmford, A., 2000. Patterns and processes in contemporary mammalian extinction. In: Entwistle, A., Dunstone, N. (Eds.), Priorities for the Conservation of Mammalian Diversity: Has the Panda had its Day? Cambridge University Press, Cambridge, UK, pp. 28–52.

Malcolm, J.R., Liu, C., Neilson, R.P., Hansen, L., Hannah, L., 2006. Global warming and extinctions of endemic species from biodiversity hotspots. Conserv. Biol. 20, 538–548.

Mei, W., Primeau, F., McWillams, J.C., Pasquero, C., 2013. Sea surface height evidence for long-term warming effects of tropical cyclones on the ocean. PNAS 110, 15207–15210.

Mora, C., Metzger1, R., Rollo, A., Myers, R.A., 2007. Experimental simulations about the effects of overexploitation and habitat fragmentation on populations facing environmental warming. Proc. Biol. Sci. 274, 1023–1028.

Owens, I.P.F., Bennett, P.M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. PNAS 97, 12144–12148.

Pearman, P.B., Guisan, A., Broennimann, O., Randin, C.F., 2007. Niche dynamics in space and time. Trends Ecol. Evol. 23, 149–158.

Pimm, S., Raven, P., Peterson, A., Sekercioglu, C.H., Ehrlich, P.R., 2006. Human impacts on the rates of recent, present, and future bird extinctions. PNAS 103, 10941–10946.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sán chez-Azofeifa, G.A., Still, C.J., Young, B.E., 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439, 161–167.

Price, S.A., Gittleman, J.L., 2007. Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. Proc. R. Soc. B 274, 1845–1851.

Purvis, A., Jones, K.E., Mace, G.M., 2000. Extinction. Bioessays 22, 1123–1133.

Raup, D.M., 1994. The role of extinction in evolution. PNAS 91, 6758–6763.

Schreiber, E.A., Burger, J., 2002. The breeding biology of seabirds. In: Schreiber, E.A., Burger, J. (Eds.), Biology of Marine Birds. CRC Press, Boca Raton, Florida, pp. 220–222.

Sekercioglu, C.H, Schneider, S.H., Fay, J.P., Loarie, S.R., 2008. Climate change, elevational range shifts, and bird extinctions. Conserv. Biol. 22, 140–150.

Shaw, T., 1938. The avifauna of Tsingtao and neighbouring districts. Bulletin of the Fan Memorial Institute of Biology (Zoology Series) 8, 133–222.

Simberloff, D., 1986. The proximate causes of extinction. In: Raup, D.M., Jablonski, D. (Eds.), Patterns and Processes in the History of Life. Springer-Verlag, Berlin, Germany, pp. 259–276.

Thomas, C.D., et al., 2004. Extinction risk from climate change. Nature 427, 145–148.

Tourism Bureau of Zhejiang Province, 2013. The outline of Zhejiang tourism statistics 2013. Available online at http://www.tourzj.gov.cn/ShowNew.aspx?id=39314 (accessed January 2015).

Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. 36, 519–539.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. Bioscience 48, 607–615.

Yan, C.W., Zhuge, Y., Chen, S.H., 2006. The Laridae and the Sternidae in China. Bird Garden of Phoenix Valley, Nantou, Taiwan.