# Climate warming and reproduction in Chinese alligators

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## Abstract

The Chinese alligator *Alligator sinensis* is a critically endangered species endemic to China, and one of the most endangered crocodilian species in the world. Like many other reptiles, important aspects of alligator biology such as foraging, timing of hibernation, breeding and the sex ratio of offspring are all affected by temperature variation. We examined the effects of long-term temperature change on oviposition dates and clutch sizes of the Chinese alligator in a semi-natural facility in southern China. Our study focused on two captive generations including an old breeding generation captured from the wild and a generation composed of their F1 offspring. Median oviposition date shifted to earlier in the year and mean clutch size was larger for both generations as the monthly mean air temperature in April increased over the 19 years of data collection. We observed a mean advance in oviposition date of 10 days for the old breeding generation from 1987 to 2005 and 8 days for both generations from 1991 to 2005. Correspondingly, clutch sizes for the two generations also increased during this period. There were no differences in median oviposition dates and clutch sizes between the two generations from 1991 to 2005. Our results suggest that Chinese alligators have responded to increasing global temperatures. Our findings also suggest that recent increasing global temperatures have the potential to have a substantial effect on Chinese alligator populations in the wild, thus prompting an urgent need for field monitoring of the effects of global warming on this endangered alligator species.

## Introduction

Many life-history features of plants and animals vary with the seasons as a result of predictable cycles in environmental conditions. In the northern hemisphere, for instance, animal migrations occur in response to large-scale climatic signals such as the North Atlantic Oscillation (Forchhammer, Post & Stenseth, 2002; Hüppop & Hüppop, 2003). At smaller scales, the timing of breeding events is often related to local, seasonal weather conditions that include the arrival of spring temperatures and the onset of snowmelt (Brown, Li & Bhagabati, 1999; Dunne, Harte & Taylor, 2003; Frederiksen *et al.*, 2004). In the last decade, there has been growing evidence demonstrating the effects of climate change on breeding in animal populations (Crick & Sparks, 1999; Dunn & Winkler, 1999; Gibbs & Breisch, 2001; Moss & Oswald, 2001). With the advent of increasing global temperatures as a result of recent human activities, some life-history features of animal populations, such as oviposition date and clutch size, have been observed to shift in relation to increasing temperatures (Janzen, 1994; Gibbs & Breisch, 2001; Torti & Dunn, 2005). Such shifts can ultimately have unexpected effects on population dynamics, species abundance and geographic distributions (Stenseth & Mysterud, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003).

The Chinese alligator *Alligator sinensis* is a critically endangered species endemic to China and is listed in Appendix 1 of China's Protection List (Jelden, 2002; Chen *et al.*, 2003; IUCN, 2004). It is one of the most endangered crocodilian species in the world. The species is restricted to Xuancheng, Nanling, Jingxian, Wuhu, Longxi and Guangde counties in the Anhui province of China (Fig. 1). Over the last few decades, the alligator population in the wild has declined from 500 individuals in the early 1980s to <120 individuals in 2005, despite considerable conservation efforts (Thorbjarnarson *et al.*, 2002). The species is threatened by loss of wetland habitats, chemical fertilizers, insecticides, hunting and increased drought and flooding (Watanabe, 1982; Chen, 1990; Zhou, 1997; Thorbjarnarson & Wang, 1999; Thorbjarnarson *et al.*, 2002; Chen *et al.*, 2003).

Reserve and captive breeding programs have been established for conserving the wild population for more than 20 years. The National Chinese Alligator Reserve (NCAR) covers almost all of the areas inhabited by alligators in Anhui province. The Anhui Research Center of Chinese Alligator Reproduction (ARCCAR) was established in 1979
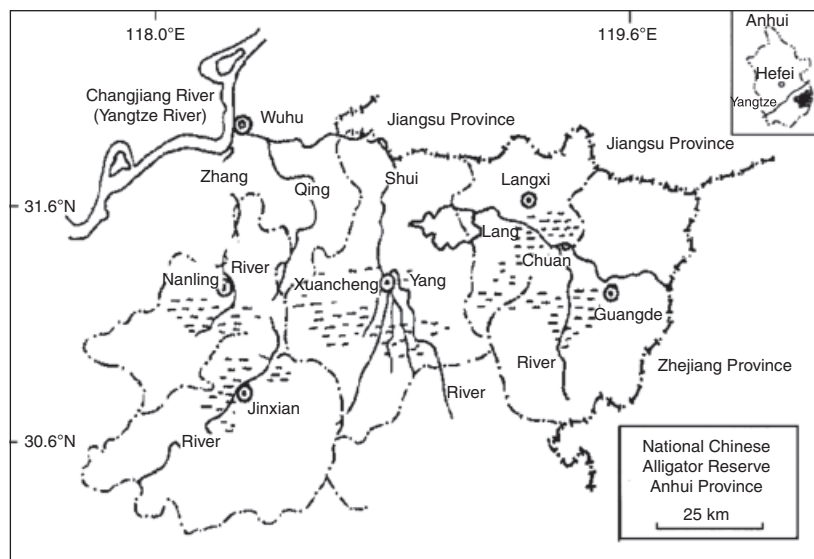
**Figure 1** Distribution of the wild Chinese alligator *Alligator sinensis* in China.

to assist captive reproduction in the alligators. Nevertheless, in the reserve, the wild alligator population has still experienced low incubation rates and low survival rates of yearling alligators (Chen *et al.*, 2003). Like many other reptiles, important aspects of alligator biology such as foraging, timing of hibernation, breeding and sex ratio of offspring are all affected by temperature variation. Understanding the effects of climate warming on these alligators is important for the conservation of the species because the small wild population of the alligators is at risk of extinction (Wang *et al.*, 1998).

There are many potential factors affecting egg-laying date under wild conditions (Brown *et al.*, 1999), including predator abundance, population density and changes in habitat quality, and it is thus difficult to control for the effects of these factors when studying wild populations. Captive populations offer some additional control that might not be found in the wild and therefore can be useful for investigating the influence of climate on life-history features. In the present study, we examined the effects of global warming on reproductive features of captive populations of Chinese alligators in ARCCAR, including variation in the timing of oviposition and clutch size.

## Methods

### Study species and area

Chinese alligators live in ponds, reservoirs and ditches and surrounding habitats in the foothills of mountains (Chen *et al.*, 2003), where there are plentiful supplies of grass and shrub cover, and a scattering of pine trees. They excavate complex burrows in banks of various waters bodies, and spend a large amount of time in burrows when sleeping, resting, reproducing and hibernating (Wang *et al.*, 1998; Chen *et al.*, 2003; Zhang *et al.*, 2005). Foraging and courtship take place in the water. Sexual maturity is reached at 5–7 years of age. Animals usually emerge from hibernation late in March or early in April when the temperature is over

16.4 °C, but do not forage until the temperature is over 20 °C. Foraging rate is associated positively with temperature (Wang *et al.*, 1998). They begin courtship activities after hibernation. The construction of nests for eggs and egg laying occurs once every year. Each animal lays its eggs within 3 h on one night. The peak time for egg laying occurs in early to mid-July (Chen *et al.*, 2003). Animals stop foraging and enter hibernation in October to early November when the temperature falls below 18 °C. Alligators in the wild have no natural predators, but are still at risk of being hunted by humans (Chen *et al.*, 2003).

ARCCAR (30°27′N, 118°30′E) is located in Xuancheng City in the reserve (30.6°–31.6°N, 118.0°–119.6°E) in Anhui Province, China. The Center, surrounded by fences *c*. 2.5 m tall, contains part of the wild habitat of the alligators in the reserve. Approximately 25% of the area is water and the other 75% is made up of hills ranging from 20 to 100 m in elevation (Wang *et al.*, 1998; Chen *et al.*, 2003; Zhang *et al.*, 2005). The Center is divided into an old breeding area for adults (Nie, Zhou & Jian, 1997), a breeding area for a young generation (F1 generation, offspring of adults in the old breeding area between 1981 and 1982), a juvenile area for offspring aged between 1 and 4 years old, and a hatching area for egg hatching and babies <1 year old. Each of the four areas is isolated from the other areas with either a fence that is 1.5 m tall or with walls of houses. Thus, individuals in an area cannot go through the fence or walls to reach other alligators. Alligators in the Center complete their lives without any artificial facilities except those provided for egg hatching and provision of food. Alligator populations in the ARCCAR originated from 76 wild adults and sub-adults, collected from the wild during 1980 and 1981 in NCAR. These individuals occupy the old breeding area (8000 m²), with no deaths and no new individuals added from either the wild or their offspring (Zhang *et al.*, 2005). Some adult alligators in the population laid eggs at ARCCAR in 1981. The F1 generation is derived from the old breeding generation. Several females also began

**Table 1** Some reproductive parameters of the old breeding population (P) from 1987 to 2005 and the F1 generation breeding population (F1) from 1991 to 2005 in ARCCAR

| Years | Old breeding population | | | | F1 generation breeding population | | | |
|---|---|---|---|---|---|---|---|---|
| | Range of oviposition date | Mean oviposition date ($\pm$ SD) | Mean clutch size* | Number of clutches | Range of oviposition date | Mean oviposition date ($\pm$ SD) | Mean clutch size* | Number of clutches |
| 1987 | 7.1–8.1 | 15.0 $\pm$ 8.5 | 28.2 | 37 | | | | |
| 1988 | 7.17–8.3 | 24.5 $\pm$ 5.8 | 25.0 | 41 | | | | |
| 1989 | 7.8–7.31 | 17.6 $\pm$ 6.3 | 28.6 | 33 | | | | |
| 1990 | 7.7–7.30 | 18.8 $\pm$ 6.7 | 27.3 | 34 | | | | |
| 1991 | 7.17–8.2 | 24.2 $\pm$ 4.8 | 24.3 | 26 | 7.16–7.26 | 22.3 $\pm$ 5.6 | 25.3 | 4 |
| 1992 | 7.15–8.1 | 23.1 $\pm$ 5.2 | 26.4 | 32 | 7.13–8.2 | 22.6 $\pm$ 5.6 | 27.5 | 38 |
| 1993 | 7.8–7.28 | 18.2 $\pm$ 6.0 | 29.4 | 30 | 7.3–7.30 | 18.0 $\pm$ 8.1 | 28.8 | 12 |
| 1994 | 6.28–7.13 | 5.8 $\pm$ 4.8 | 23.6 | 37 | 6.28–7.20 | 7.4 $\pm$ 6.3 | 26.2 | 34 |
| 1995 | 7.14–7.28 | 21.0 $\pm$ 4.5 | 24.5 | 23 | 7.9–7.29 | 20.0 $\pm$ 6.0 | 27.6 | 22 |
| 1996 | 7.15–8.2 | 23.5 $\pm$ 5.7 | 23.0 | 23 | 7.3–8.1 | 21.1 $\pm$ 7.9 | 22.7 | 51 |
| 1997 | 6.28–7.28 | 14.4 $\pm$ 8.1 | 26.0 | 28 | 6.29–7.31 | 16.7 $\pm$ 8.9 | 24.4 | 112 |
| 1998 | 6.29–7.18 | 8.06 $\pm$ .5 | 31.0 | 7 | 6.30–7.27 | 11.6 $\pm$ 7.5 | 28.8 | 82 |
| 1999 | 7.7–7.23 | 17.6 $\pm$ 6.1 | 26.1 | 7 | 7.9–7.29 | 20.7 $\pm$ 5.3 | 26.3 | 50 |
| 2000 | 7.5–7.31 | 13.8 $\pm$ 7.7 | 25.9 | 13 | 6.30–7.31 | 17.8 $\pm$ 8.5 | 29.4 | 73 |
| 2001 | 7.2–7.23 | 7.3 $\pm$ 6.7 | 31.8 | 10 | 7.4–8.2 | 17.1 $\pm$ 7.5 | 29.0 | 59 |
| 2002 | 7.5–7.26 | 13.9 $\pm$ 6.6 | 29.1 | 11 | 7.5–7.28 | 18.0 $\pm$ 6.3 | 30.0 | 49 |
| 2003 | 7.13–7.23 | 16.8 $\pm$ 4.4 | 32.0 | 4 | 6.29–7.27 | 13.0 $\pm$ 9.8 | 31.8 | 28 |
| 2004 | 7.9–7.20 | 14.6 $\pm$ 4.5 | 32.0 | 5 | 6.27–8.1 | 12.7 $\pm$ 9.3 | 34.7 | 58 |
| 2005 | 6.21–7.14 | 2.4 $\pm$ 7.4 | 32.3 | 11 | 6.25–7.16 | 5.7 $\pm$ 6.4 | 35.2 | 66 |

The mean oviposition date began at 1 July.

*SD was not provided because original data were recorded as number of total eggs and number of clutches a day.

ARCCAR, Anhui Research Center of Chinese Alligator Reproduction.

to produce eggs in 1988. Alligator eggs were incubated in the artificial hatching area.

Our study focused on the old breeding generation population and the F1 generation breeding population (reproductive data on the F2 generation breeding population do not cover a long enough time span in order to perform an adequate analysis). The two populations occupy similar habitats (both are a part of the wild alligator habitat), have a similar population density (5.8 individuals 1000 m$^{-2}$ for the old breeding generation, 6 individuals 1000 m$^{-2}$ for the F1 generation; male:female sex ratio $\approx$ 1:4 for both populations) and are provided with the same kind of food (alligator populations are provided with fish every 2 days). The quantity of food provisioned for the two populations was based on the number and average weight of alligators through the seasons (Chen et al., 2003): 2–3% of the average weight for alligators in April–May, 4–5% from June to July, 6–7% between August and mid-September and 3–4% after late September. Alligators are provided with food in spring at a fixed time every year (around 6 May). At this time the air temperature generally exceeds 20 °C. The provision of food ceases when the temperature falls below 20 °C between 25 October and 5 November in autumn. No humans were allowed to enter breeding areas except between 12:00 and 14:00 h when eggs were collected.

## Oviposition date

During late June, breeding areas were checked for eggs daily by ARCCAR keepers. Eggs were taken to the artificial hatching area for artificial incubation. We collected data on all females from the old generation and the F1 generation that had matured at least 2 years previously. We only used data collected after the management of the populations became standardized and systematic, thus excluding other data collected (i.e. before 1987). We analyzed reproductive data spanning 19 years (1987–2005) for the old breeding generation and 15 years (1991–2005) for the F1 generation breeding population. We used median oviposition date and mean clutch size per year as indictors of oviposition date and clutch size for the alligators in each year. Median dates are considered to be more reliable measures of breeding phenology than the date that the first egg is laid (Crick & Sparks, 1999; Frederiksen et al., 2004). Table 1 details parameters related to median oviposition date and mean clutch size.

## Climatic data

We collected climatic data from Xuancheng meteorological station located 1.5 km from ARCCAR to test relationships between climatic conditions and median oviposition date and mean clutch size. The station belongs to one of national meteorological stations for long-term meteorological monitoring in China. The principle climate variables we used were monthly mean air temperature, monthly maximum and minimum air temperature in the months preceding breeding from March to June. The March–June period

covered all months that alligators emerged from hibernation before producing eggs.

## Statistical analyses

Initially, we determined whether climatic variables had changed from 1987 or 1991 to 2005, as well as over the past 50 years using simple regressions. Then, we tested if oviposition date and mean clutch size had changed from 1987 to 2005 for the old breeding population and from 1991 to 2005 for both the old breeding population and the F1 generation breeding population, again using simple regressions. We used regressions to examine the relationship between median oviposition date or mean clutch size and each of the climatic variables (monthly mean air temperature, and monthly maximum and minimum air temperature from March to June during 1987–2005 or 1991–2005). Finally, we implemented stepwise multiple-variable regressions to determine relationships between reproduction and air temperature with median oviposition date or mean clutch size as the response variable and monthly mean air temperature, monthly maximum and minimum air temperature as the independent variables. The stepwise multiple-variable regressions allowed the selection of a subset of independent variables that significantly affected the response variable.

One potential problem was that body mass or age could have affected oviposition date and clutch size, which might have confounded the effect of temperature. Data on body mass and age in both populations were not available for most years. However, individuals of the old breeding population are generally much heavier and older than those of the F1 generation breeding population. For instance, in 1991 the body weight of males in the F1 generation breeding population was <74% of those in the old breeding population and the body weight of females in the F1 generation breeding population was <87% of those in the old breeding population (Ma, 2005). If body mass or age had an effect on oviposition date or clutch size, there should be a difference in oviposition date and mean clutch size between the two populations during the same year. If there was no effect of body mass or age, then oviposition date and clutch size should respond linearly to temperature in the same way for both populations. We tested if there was a difference in oviposition date and clutch size during the 1991–2005 period between the old breeding population and the F1 generation breeding population using paired *t*-tests. We examined if there was a similar linear trend in median oviposition date and mean clutch size in relation to temperature from 1991 to 2005, between the two different generations of populations, using simple regressions. For all statistical analyses, the significance level was set at $\alpha = 0.05$.

## Results

Mean air temperatures in March and April increased significantly at ARCCAR during 1987–2005 ($r^2 = 0.390$, $n = 19$, $P = 0.004$ for March; $r^2 = 0.342$, $n = 19$, $P = 0.009$ for April) (Fig. 2a–d), with the same trend observed during the 1991–2005 period ($r^2 = 0.490$, $n = 15$, $P = 0.004$ for March; $r^2 = 0.278$, $n = 15$, $P = 0.043$ for April). Mean temperatures in April also increased over the longer period of the last 50 years ($r^2 = 0.162$, $n = 50$, $P = 0.004$, Fig. 2e). There were no such changes in either minimum temperature or maximum temperature in March and April (e.g. $r^2 = 0.074$, $n = 19$, $P = 0.259$ for maximum temperature in March between 1987 and 2005; $r^2 = 0.029$, $n = 19$, $P = 0.478$ for minimum temperature in April between 1987 and 2005). Furthermore, there were no changes in all three temperature indices in either May or June (e.g. $r^2 = 0.081$, $n = 19$, $P = 0.238$ for mean temperature in May between 1987 and 2005; $r^2 = 0.232$, $n = 15$, $P = 0.069$ for mean temperature in June between 1991 and 2005).

The median date of oviposition of Chinese alligators at ARCCAR advanced by 10.8 days from 1987 to 2005 for the old breeding generation (Fig. 3a). Over the same period, mean clutch sizes increased significantly (Fig. 3b). From 1991 to 2005, the median date of oviposition also advanced for both generations (old breeding generation by 9.0 days, F1 generation by 8.4 days), and mean clutch sizes increased significantly (Fig. 4a–d).

Simple regressions showed that median oviposition date was negatively correlated with mean temperature in March and April and that mean clutch size was positively correlated with mean temperature in April for the old breeding generation, between 1987 and 2005 (Table 2). From 1991 to 2005, median oviposition date was negatively associated with mean temperature in March and April and maximum temperature in April for the old breeding generation (Table 3). Similarly, mean temperature and maximum temperature were negatively associated with median oviposition date in April for the F1 generation (Table 3). Mean clutch size was positively related to April mean temperature for both generations during this period. However, stepwise multiple-variable regressions indicated that only mean air temperature in April could explain significant and unique variation in median date of oviposition and mean clutch size for the old breeding generation from 1987 to 2005 (Table 2) and for both generations during 1991–2005 (Table 3). In summary, our results showed that median oviposition date shifted to earlier in the year and mean clutch size was larger as the monthly mean air temperature in April increased over the 19 years of data collection.

The relationship between median date of oviposition and mean clutch size was negative and significant for the old breeding generation from 1987 to 2005 ($r^2 = -0.301$, $n = 19$, $P = 0.015$), and for both generations from 1991 to 2005 ($r^2 = -0.396$, $n = 15$, $P = 0.012$ for the old breeding generation; $r^2 = -0.281$, $n = 15$, $P = 0.004$ for the F1 generation). Thus, clutch sizes became larger when oviposition date shifted to earlier in the year.

Paired *t*-tests showed that there was no difference in median oviposition dates and mean clutch sizes between the two generations during 1991–2005 ($t = 0.894$, d.f. = 28, $P = 0.379$ for oviposition date; $t = 0.546$, d.f. = 28, $P = 0.589$ for clutch size). During 1991–2005, oviposition dates were positively correlated between the two generations
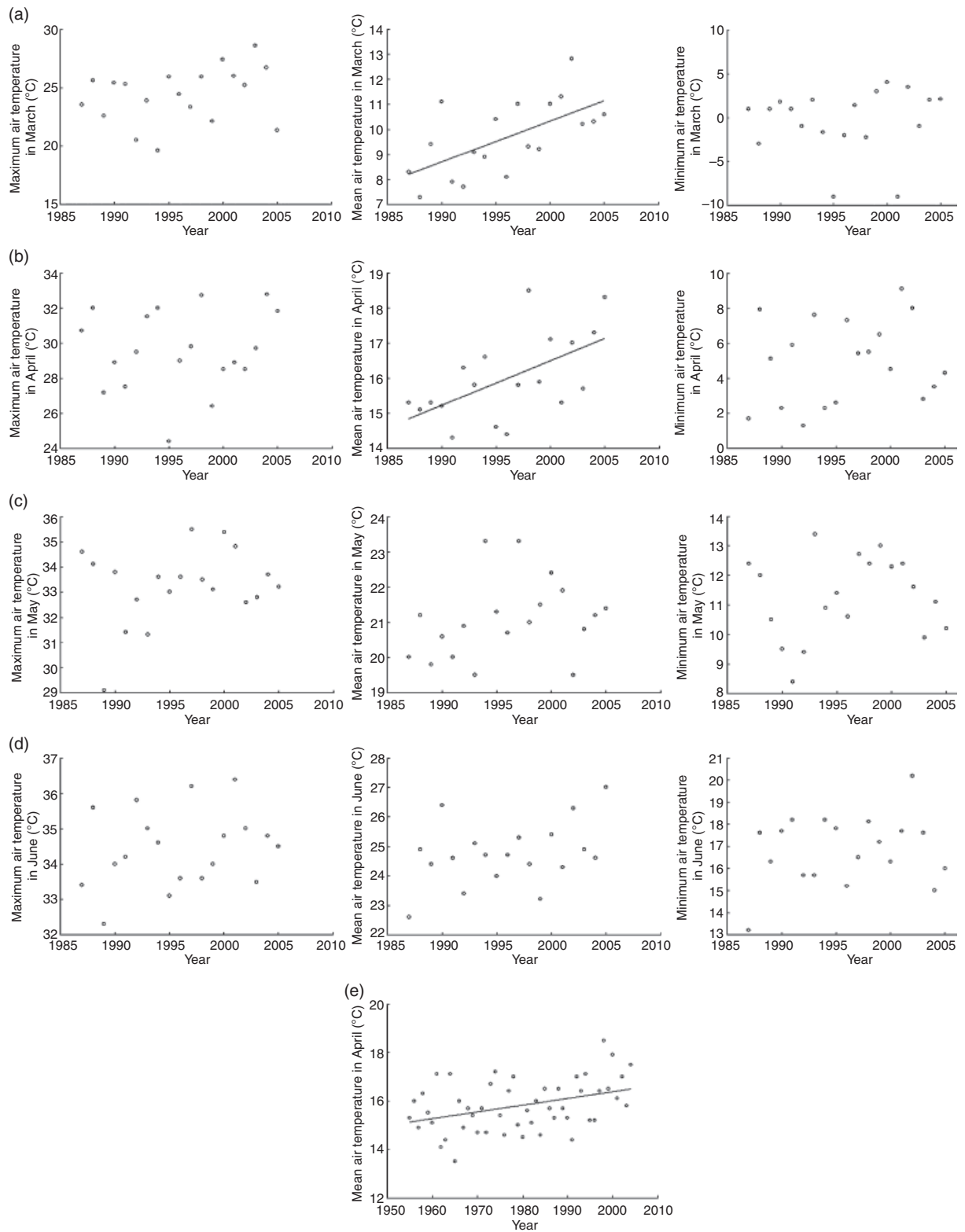
**Figure 2** Change in air temperature in March–June from 1987 to 2005 in ARCCAR [(a) March; (b) April; (c) May and (d) June] and change in April mean air temperature from 1955 to 2004 (e).
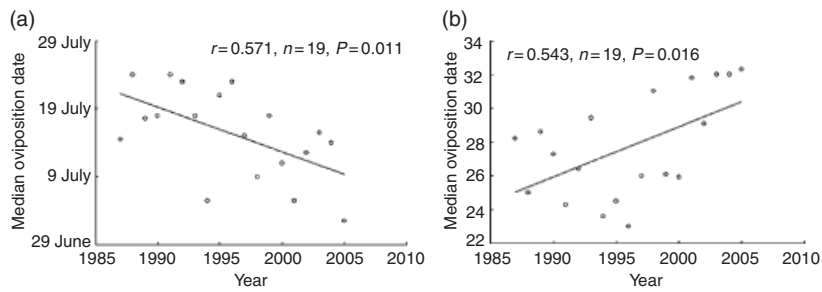
**Figure 3** Changes in median oviposition date and mean clutch size for the old breeding population from 1987 to 2005. (a) Change in median oviposition date; (b) change in mean clutch sizes. Lines represent linear regressions.
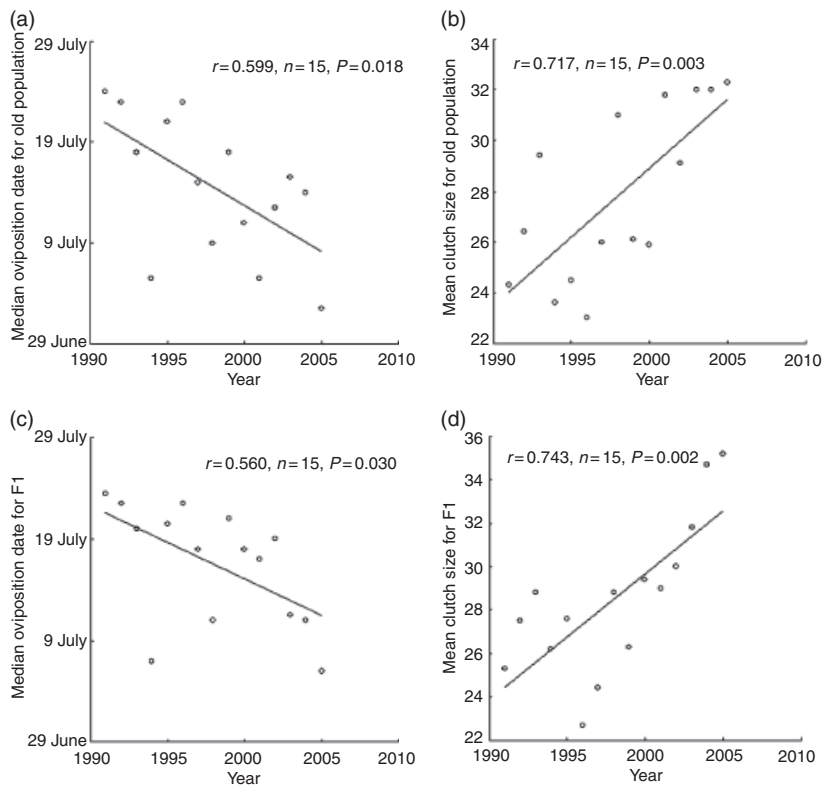


**Figure 4** Changes in median oviposition date and mean clutch size for the old generation and the F1 generation from 1991 to 2005. (a) Change in median oviposition date for the old generation; (b) change in mean clutch size for the old generation; (c) change in median oviposition date for the F1 generation; (d) change in mean clutch sizes for the F1 generation.

($r^2 = 0.656$, $n = 15$, $P < 0.001$), as were clutch sizes ($r^2 = 0.691$, $n = 15$, $P < 0.001$).

## Discussion

Our results provide evidence that Chinese alligators have shifted their timing of oviposition. The old breeding generation showed advances in the median date of oviposition by 10.8 days from 1987 to 2005; both the old breeding generation and the F1 generation advanced their median dates of oviposition by 9.0 and 8.4 days, respectively, from 1991 to 2005, with associated increases in clutch size. These changes were related to increases in air temperatures in April. Although mean air temperature in hibernating March also increased from 1991 to 2005, it did not affect oviposition

date and clutch size, possibly because in most of March, the alligators were in hibernation in burrows. Mean temperatures in March are below 13 °C (Fig. 2a). At such low temperatures, alligator metabolism is inhibited and assimilation of food is not possible (Lance, 2003). Our results are in agreement with a number of studies on the relationship between phenology and increasing air temperatures performed on mammals, birds, reptiles and amphibians (Beebe, 1995; Forchhammer *et al.*, 1998; Brown *et al.*, 1999; Crick & Sparks, 1999; Blaustein *et al.*, 2001; Gibbs & Breisch, 2001; Walther *et al.*, 2002; Sergio, 2003; Both & Visser, 2005; Gordo, Brotons & Ferrer, 2005; Sparks, Bairlein & Bojarinova, 2005; Torti & Dunn, 2005; Chamaille-Jammes *et al.*, 2006; Hawkes, Broderick & Godley, 2006; Møller, Flensted-Jensen & Mardal, 2006). Our results also support the suggestion of Reading (1998) and Blaustein (2001) that increases in air

**Table 2** Results of single-variable regressions and the stepwise multiple-variable regressions relating reproductive parameters (median oviposition date, mean clutch size) to temperature for the old breeding population from 1987 to 2005

| | | Median oviposition date | | | | Mean clutch size | | | |
| | | Single regression | | Multiple regression | | Single regression | | Multiple regression | |
| Months | Temperature (°C) | R | P | B | P | R | P | B | P |
|---|---|---|---|---|---|---|---|---|---|
| March | Mean | −0.536 | **0.018** | −0.339 | 0.065 | 0.444 | 0.057 | 0.293 | 0.183 |
| | Min. | −0.024 | 0.923 | 0.252 | 0.185 | 0.077 | 0.753 | −0.131 | 0.564 |
| | Max. | 0.121 | 0.623 | 0.043 | 0.814 | 0.280 | 0.246 | 0.345 | 0.092 |
| April | Mean | −0.695 | **0.001** | −0.695 | **0.001** | 0.545 | **0.016** | 0.545 | **0.016** |
| | Min. | 0.009 | 0.970 | −0.067 | 0.715 | 0.054 | 0.825 | 0.115 | 0.548 |
| | Max. | 0.397 | 0.092 | −0.014 | 0.951 | 0.393 | 0.096 | 0.128 | 0.615 |
| May | Mean | −0.413 | 0.079 | −0.275 | 0.127 | −0.225 | 0.355 | −0.360 | 0.109 |
| | Min. | 0.256 | 0.290 | −0.126 | 0.496 | 0.117 | 0.635 | 0.011 | 0.959 |
| | Max. | 0.310 | 0.197 | −0.198 | 0.276 | 0.067 | 0.786 | −0.164 | 0.445 |
| June | Mean | −0.331 | 0.166 | −0.112 | 0.562 | 0.220 | 0.366 | 0.043 | 0.850 |
| | Min. | 0.105 | 0.670 | −0.063 | 0.729 | 0.068 | 0.782 | −0.101 | 0.635 |
| | Max. | 0.165 | 0.499 | −0.061 | 0.742 | 0.051 | 0.836 | −0.033 | 0.878 |

*B* represents standardized coefficients from regression models. Significant results in bold.
Min., minimum; max., maximum.

**Table 3** Results of single-variable regressions and stepwise multiple-variable regressions relating reproductive parameters (median oviposition date, mean clutch size) to temperature for the old breeding population and the F1 generation breeding population from 1991 to 2005

| | | Median oviposition date | | | | Mean clutch size | | | |
| | | Single regression | | Multiple regression | | Single regression | | Multiple regression | |
| Months | Temperatures (°C) | R | P | B | P | r | P | B | P |
|---|---|---|---|---|---|---|---|---|---|
| *Old breeding population* | | | | | | | | | |
| March | Mean | −0.534 | **0.041** | −0.353 | 0.099 | 0.453 | 0.090 | 0.307 | 0.217 |
| | Min. | 0.010 | 0.971 | 0.346 | 0.122 | 0.040 | 0.887 | −0.225 | 0.393 |
| | Max. | −0.094 | 0.739 | 0.010 | 0.963 | 0.343 | 0.211 | 0.418 | 0.068 |
| April | Mean | −0.684 | **0.005** | −0.684 | **0.005** | 0.559 | **0.030** | 0.559 | **0.030** |
| | Min. | −0.077 | 0.786 | −0.2.09 | 0.330 | 0.138 | 0.624 | 0.249 | 0.306 |
| | Max. | −0.520 | **0.047** | −0.121 | 0.672 | 0.506 | 0.054 | 0.241 | 0.453 |
| May | Mean | −0.446 | 0.097 | −0.358 | 0.078 | −0.224 | 0.423 | −0.305 | 0.199 |
| | Min. | −0.289 | 0.297 | −0.158 | 0.468 | 0.150 | 0.594 | 0.039 | 0.875 |
| | Max. | −0.446 | 0.096 | −0.319 | 0.127 | −0.003 | 0.991 | −0.123 | 0.620 |
| June | Mean | −0.509 | 0.053 | −0.270 | 0.240 | 0.333 | 0.226 | 0.119 | 0.657 |
| | Min. | −0.201 | 0.472 | −0.203 | 0.335 | −0.023 | 0.936 | −0.021 | 0.932 |
| | Max. | −0.253 | 0.362 | −0.194 | 0.361 | 0.174 | 0.5.5 | 0.125 | 0.609 |
| *F1 generation breeding population* | | | | | | | | | |
| March | Mean | −0.251 | 0.366 | −0.036 | 0.872 | 0.457 | 0.087 | 0.281 | 0.222 |
| | Min. | −0.042 | 0.883 | 0.288 | 0.199 | 0.187 | 0.505 | −0.90 | 0.716 |
| | Max. | 0.089 | 0.753 | 0.003 | 0.987 | 0.256 | 0.356 | 0.341 | 0.114 |
| April | Mean | −0.693 | **0.004** | −0.693 | **0.004** | 0.643 | **0.010** | 0.643 | **0.010** |
| | Min. | 0.335 | 0.222 | 0.215 | 0.309 | −0.205 | 0.463 | −0.91 | 0.693 |
| | Max. | −0.692 | **0.004** | −0.416 | 0.122 | 0.423 | 0.116 | −0.003 | 0.991 |
| May | Mean | −0.379 | 0.163 | −0.291 | 0.157 | −0.157 | 0.577 | −0.249 | 0.262 |
| | Min. | 0.015 | 0.956 | 0.161 | 0.452 | −0.054 | 0.848 | −0.191 | 0.400 |
| | Max. | −0.218 | 0.436 | −0.079 | 0.715 | −0.048 | 0.865 | −0.188 | 0.408 |
| June | Mean | −0.428 | 0.111 | −0.167 | 0.470 | 0.446 | 0.095 | 0.215 | 0.380 |
| | Min. | −0.027 | 0.924 | −0.029 | 0.892 | −0.096 | 0.736 | −0.094 | 0.677 |
| | Max. | 0.083 | 0.768 | 0.147 | 0.488 | 0.009 | 0.759 | −0.049 | 0.828 |

*B* represents standardized coefficients from regression models. Significant results in bold.
Min., minimum; max., maximum.

temperatures 1–2 months immediately before breeding may affect the timing of breeding, as reported for amphibians.

It is predicted that earlier breeding by increasing temperature may lead to larger clutches (Winkler, Dunn & McCulloch, 2002). This prediction is based on a general pattern in the life histories of many birds that females laying later in the breeding season tend to lay smaller clutches due to decreasing food availability or reducing offspring survival prospects or increasing predation risk with the season (see Bêty, Gauthier & Giroux, 2003, for a review). Our results are consistent with this prediction (Winkel & Hudde, 1997; McCleery & Perrins, 1998; Crick & Sparks, 1999). Many studies have shown that when climate change has led to an advancement of the availability of the main food sources of the study animal, individuals are expected to breed earlier (Crick *et al.*, 1997; Winkel & Hudde, 1997; McCleery & Perrins, 1998; Crick & Sparks, 1999). For the captive populations of Chinese alligators, however, the timing of first provision in spring (6 May) did not vary over time in the study period, suggesting that the timing of food sources is not the main reason for the earlier timing of oviposition and larger clutches. The earlier timing and larger clutches associated with increasing temperature for the alligators may be due to changes in the reproductive cycle and energy expenditure. Like other alligators (see Lance, 2003), the reproductive cycle of Chinese alligators is closely tied to an annual thermal cycle (Chen *et al.*, 2003). Increasing mean temperature in April may promote courtship activities after hibernation and make the female alligators commence a vitellogenic period early (Lance, 2003). This may lead to earlier laying date and larger clutch size. The warmer April temperatures may decrease energy expenditure in relation to thermoregulation, allowing females to accumulate sufficient body reserves for earlier oviposition or for larger clutch sizes in the breeding season. Studies have found that accumulation of body reserves is linked to date of oviposition in reptiles (Corkett & McLaren, 1978; Gans & Crews, 1992; Pough *et al.*, 2001), which could affect clutch size. It is also possible that the alligators are being fed later each year due to warmer autumns, which may increase in fecundity. The provision of food ceases when the temperature falls below 20 °C in autumn. Eating later in the year could result in more fat stores (due to a shorter hibernation period), which might actually increase clutch size next year. This possibility warrants a further study. Other factors, such as predators, natural disasters, human activities, changes in habitat quality, population density and management practice, are unlikely to affect the timing of breeding and clutch sizes in the alligators we studied. There have been few changes in habitat quality, population density and management practice during the study period (Chen *et al.*, 2003).

A number of studies have documented that experienced, larger breeding birds lay eggs earlier, and lay larger clutches or larger eggs than inexperienced, young birds (Nol & Smith, 1987; Schiegg *et al.*, 2002; Heezik *et al.*, 2002). Contrary to these birds, body size, age and breeding experi-ence in the alligators have little effect on advancement in oviposition date and increases in clutch size. Individuals in the old breeding generation are generally larger in body size or age and have more breeding experience than the offspring generation. However, oviposition date and clutch size do not differ between the two generations. Furthermore, oviposition dates and clutch sizes for both generations are positively related. These patterns arise possibly because alligators repeatedly use the same nest site for breeding each year (Chen *et al.*, 2003). There has not been much change in the quality of habitats under protection over time, so the alligators could find the nest site easily each year. Older alligators generally lay larger eggs than young but do not have a larger clutch size (Wang & Xia, 2005). Chinese alligators may be similar to some anoles and eublepharid geckos with fixed clutch size (Kratochvíl & Kubicka, 2007; Uller & Olsson, 2007). In such reptile species, pelvic girdle structure constrains egg size, and the egg size generally increases with body size of females.

There has been a warming trend in April over the past 50 years in the reserve. Such a trend may have important effects on conservation of the wild population of Chinese alligators. Our results showed that captive populations of Chinese alligators with regular food provisioning lay eggs earlier and increase clutch size in response to increasing temperatures. If the peak date of food availability of wild Chinese alligators matched their phenology, then a warmer climate might benefit wild alligators. These benefits include laying larger clutch sizes, increasing the number of offspring and extending the period of growth for offspring (Sanz, 2002). However, if the peak of food availability does not match alligator phenology, then adult alligators and young, newly hatched alligators could face immediate food shortages, which would provide a serious threat for the wild alligator population. The advancement of oviposition date might negatively affect developmental rates of alligator's eggs and offspring sex ratio. Some studies have suggested that lower temperatures in the early period of development reduce the incubation rate of eggs and offspring sex ratio (males vs. females) in the wild (He *et al.*, 2002). As there has been no increase in July temperatures from 1950 to 2005, earlier oviposition could lead to earlier egg incubation. Oviposition date for the captive populations had moved 10 days earlier in the year from 1987 to 2005. Correspond-ingly, the peak time of egg incubation would shift from early–mid July to later June–early July. The temperature in early July is 1.8 °C lower than the middle of July (unpubl. data). Such declines in temperature might result in a serious reduction in developmental rates of eggs and offspring sex ratio.

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