
EFFECTS OF ENVIRONMENTAL TEMPERATURE ON THE ONSET AND THE DURATION OF OVIPOSITION PERIOD OF *CAIMAN LATIROSTRIS*

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Abstract.—Reproductive biology of Broad-snouted Caiman (*Caiman latirostris*) may be affected by climatic variables. However, it remains unknown which are the specific climatic variables that affect the onset of oviposition, as well as its duration. In this study, we use a series of climatic data corresponding to the preceding four weeks to oviposition to know which of them influence these reproductive characteristics, and we observed that weather conditions of the immediate week prior to oviposition was the most important factor. We found a delay in the onset of oviposition positively associated to the number of days with temperatures below 20° C in the previous weeks. Conversely, we found that oviposition starts earlier with the increase of the number of days with temperatures above 33° C during the previous week. Additionally, the duration of the oviposition period is longer when the number of days with temperatures above 33° C increases. No relationship was found between the onset of oviposition and the number of storms or the amount of rainfall in the four preceding weeks. We also noted that in seasons when the start of oviposition is delayed, the duration of oviposition of this period is shorter. The onset of oviposition of female *C. latirostris* may vary by up to three weeks among years. The information obtained here is a useful tool for managing strategies for its predictive power of the timing and duration of oviposition based on climatic information.

Key Words.—Broad-snouted Caiman; climate variables; clutch; eggs; nesting onset

INTRODUCTION

Climate at temperate extremes, such as in Santa Fe, Argentina (latitude 31° S) may constrain activity and other aspects for large ectotherms, such as Broad-snouted Caiman (*Caiman latirostris*). Natural history parameters that may be influenced are the timing and length of the breeding season, embryonic development, and growth (Shine et al. 2003). It was reported that small lizards living in higher latitudes are exposed to energetic limitations, affecting some life history traits, such as sexual maturation, clutch size, offspring size, reproductive effort, fecundity, and timing or duration of reproductive events (Angilletta et al. 2009; Medina and Ibargüengoytia 2010). Therefore, it is expected that other reptiles inhabiting these regions may be similarly affected by climatic conditions.

Previous studies reported that nesting characteristics of many oviparous species may be affected by weather conditions (Walther et al. 2002; Telemeco et al. 2009). Additionally, some populations of turtles and alligators nest earlier

when ambient temperature and water availability increase (Joanen 1969; Crawshaw and Schaller 1980; Forchhammer et al. 1998; Weishampel et al. 2004). Thus, it is reasonable to postulate that the onset and duration of oviposition of *Caiman latirostris* is also a function of environmental factors, as noted in the closely related American Alligator (*Alligator mississippiensis*, Joanen 1969).

The southern distribution limit of *C. latirostris* is Santa Fe Province, Argentina. In Santa Fe Province, caiman populations live in a temperate climate that restricts the activity season to the warmer months of the year (from late September to early April, spring-summer in the southern hemisphere, Siroski 2004). In fact, the reproductive biology of this oviparous ectotherm is strongly cyclic. However, it remains unknown if the onset and length of the oviposition period is influenced by some specific climatic factor. Oviposition takes place in December (Larriera and Imhof 2006), suggesting a relationship between weather conditions and nesting onset and duration. For example, extreme

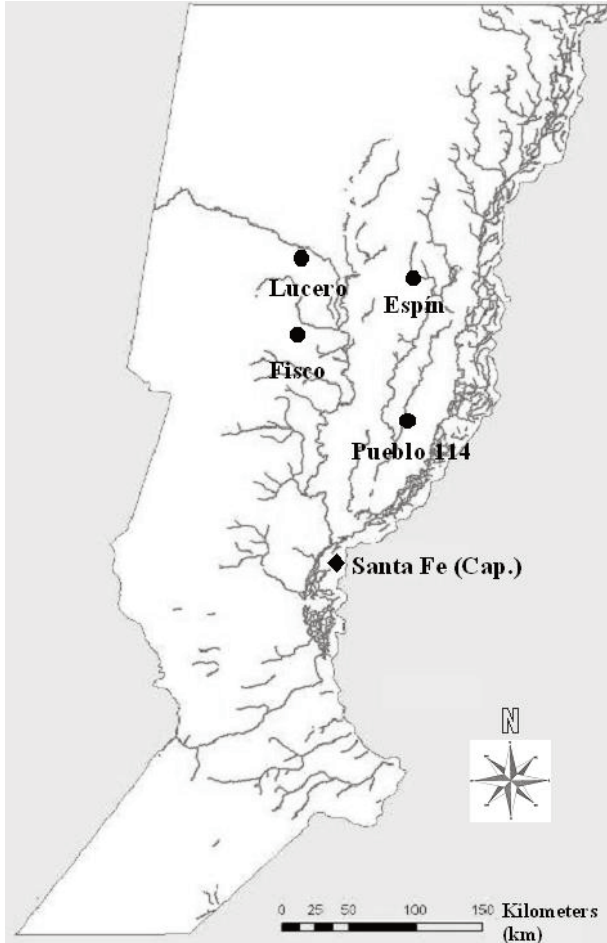


Figure 1. The four study sites of Broad-snouted Caiman (*Caiman latirostris*) in Santa Fe Province, Argentina.

temperatures during oviposition may affect the duration of incubation period (Piña et al. 2003), hatching success (Matsuzawa et al. 2002; Doody 2011), growth and survival of hatchlings (Altwegg et al. 2005), and sex determination (Piña et al. 2003).

To determine the role of climate on the onset and length of oviposition in *C. latirostris* in the southern extreme of its distribution we aim to answer the following questions: 1) is there variation in the onset of oviposition period of *C. latirostris* among reproductive seasons?; 2) which climatic factors (including photoperiod) determine the onset of oviposition?; and 3) is the duration of the oviposition period related to the onset of oviposition? This information may be useful for the conservation and management of this species, currently under ranching management in Argentina (i.e., eggs are collected and artificially incubated). This knowledge may help as an estimation of caiman females reproduction, and also help to coordinate future harvesting activities, reducing nest losses by flooding, drought, or depredation.

MATERIALS AND METHODS

We studied *Caiman latirostris* breeding populations in four sites in northern Santa Fe Province (Fig. 1). The study sites were: Estancia El Lucero (S 29° 55' W 60° 55'), Reserva

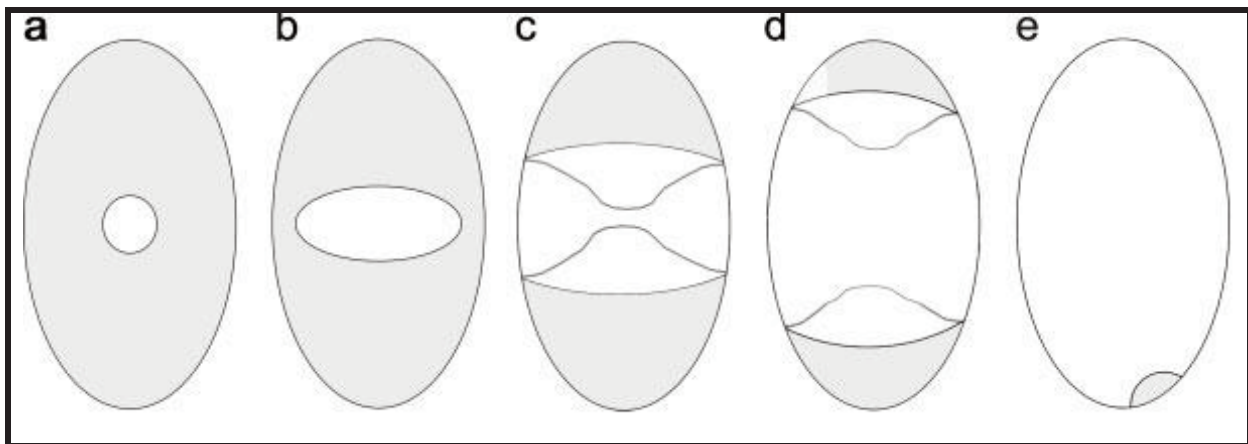


FIGURE 2. Images of the upper side of eggs of Broad-snouted Caiman (*Caiman latirostris*) and the development of the opaque patch throughout incubation at 31° C. (a) at day 2 the patch is just a white dot in the top of the egg; (b) at day 3 the patch has increased in area, both in width and length; (c) by day 4 the patch has covered the minimum diameter of the egg; (d) approximately at day 36 of incubation at 31° C the patch have covered about 70 % of the egg; finally (e) by day 57 the patch have covered almost a 100% of the egg (from Iungman et al. 2008).

Natural FISCO (S 30° 15' W 60° 55'), Pueblo 114 (S 30° 40' W 60° 20') and Espin Stream (S 29° 58' W 60° 05'). From 2006 to 2009 (four reproductive seasons), we located 292 nests with eggs (Pueblo 114: n = 18; Espin: n = 19; Fisco: n = 185; Lucero: n = 70). In each year, we searched for nests from early December until no more new nest were found. We determined approximate time of oviposition by examining the eggs and the presence and size of the opaque band (at least 15 eggs per nest, selected from different parts of the clutch chamber), which is an indicator of the embryo development (Iungman et al. 2008; Fig. 2). This method is based on measuring the growth (length and width) of the opaque band on the egg that takes place during incubation (Iungman et al. 2008; Antelo et al. 2010), constituting a useful tool to estimate the oviposition time without killing the embryo with an acceptable accuracy (± 2 d). However, it is a good estimator only up to the first 10 d of incubation, after which opaque band development shows great variability (Donayo et al. 2002). Oviposition periods were presented in 1-week intervals. We started to collect environmental data one month before the onset of oviposition, during the first week of November (2–9 November November; Table 1), considering that this species starts oviposition in mid December (Larriera and Imhof 2006). For every nesting season we recorded harvesting date, site, and microhabitat. During the same period of time, we recorded daily minimum and maximum air temperatures using dataloggers (HOBO Temp data loggers, Onset Computer Corporation, Bourne, Massachusetts, USA). We also used local daily meteorological information of rainfall (number of storms and amount of precipitation in mm) provided by Facultad de Ingeniería y Ciencias Hídricas (Universidad Nacional del Litoral), the government of the Santa Fe Province (Available at <http://www.santa-fe.gov.ar/gbrn/regpluv/>) and the Servicio Meteorológico Nacional Argentino (<http://www.smn.gov.ar>).

To assess the relationship between climatic conditions during the four weeks prior to the first documented oviposition in each reproductive season, the beginning of oviposition, and its duration, we built a database with the following

TABLE 1. Classification in weeks of the onset of oviposition period of Broad-snouted Caiman (*Caiman latirostris*) from northern Santa Fe Province, Argentina, assigning as week 1 the period from 2–9 November and successive weeks.

Week	Dates
1	2 Nov-9 Nov
2	10 Nov-17 Nov
3	18 Nov-25 Nov
4	26 Nov-3 Dec
5	4 Dec-11 Dec
6	12 Dec-19 Dec
7	20 Dec-27 Dec
8	28 Dec-4 Jan
9	5 Jan-12 Jan
10	13 Jan-20 Jan
11	21 Jan-28 Jan
12	29 Jan-4 Feb

variables: number of days with temperatures below 20° C; number of days with mean temperatures above 25° C; number of days with temperatures above 33° C; number of storm events; amount of rainfall (mm precipitation); the starting oviposition week, and the duration of the oviposition period (weeks between first and last oviposition during the entire study). Because photoperiod is constant among years, it was not included in the data matrix. We recorded these data corresponding to the four weeks preceding the first oviposition event at each study site for the four seasons (2006–2009). We evaluated only the four weeks prior to the first oviposition because our aim was to establish which environmental variables triggers nesting, and not follicular development, though these are likely related. We examined if initiation of oviposition was similar among seasons and sites by Kruskal-Wallis test.

We analyzed data with principal components analysis (PCA), and variables were automatically transformed, using InfoStat (Di Rienzo et al. 2008). We considered associations between variables to be significant when eigenvectors were greater than 0.60. For further analysis, we selected the week that better explained data variation. Using only that week,

we studied the relationships found among variables by simple regression (variables that met assumptions of normality and homoscedasticity). Within the regression analysis, we excluded those data with a high leverage and high standardized residuals (Sokal and Rohlf 1995). If the assumptions were not reached, we used Spearman ranks correlation (r_p).

RESULTS

We found that initiation of oviposition of *C. latirostris* from all study sites differed by up to three weeks among years. The earliest first date of oviposition was 12 December (2006 in Fisco and 2007 in Lucero) and the latest first date of oviposition was on 5 January (2008 in Lucero, 2006 and 2007 in Pueblo 114, 2007 and 2008 in Espin), encompassing a range of three weeks among years and sites. Considering the four years of this study, length of the oviposition period was six weeks (from 12 December to 29 January), with an average duration of 2.8 ± 1.2 weeks (range one to five weeks; Fig. 3).

Peak of ovipositions took place between 5 January and 12 January. This was observed at most of the sites except for Pueblo 114 in 2008/2009, where oviposition occurred between 12–19 December. It was also observed that sites sharing river basins, (such as Espin and Pueblo 114, and Fisco and Lucero) showed similar trends regarding the initiation and duration of oviposition (Fig. 3). We did not observe a significant relationship between the start and duration of oviposition period with photoperiod (all $r^2 < 0.01$, $P > 0.120$), and oviposition dates varied among years ($H = 81.1$, $df = 3$, $P < 0.001$) and sites ($H = 125.9$, $df = 3$, $P < 0.001$). We noted in some cases that the onset of oviposition occurred prior to the longest photoperiod (21 December), but in every year nearly 75 % of the clutches were deposited after 21 December.

Climatic conditions of the previous four weeks influenced start and duration of oviposition (PCA), but weather conditions in the week prior to oviposition had the greatest influence (Table 2). The start of oviposition (week, eigenvector = 0.87) was delayed with increasing of number of days with temperatures below of 20° C

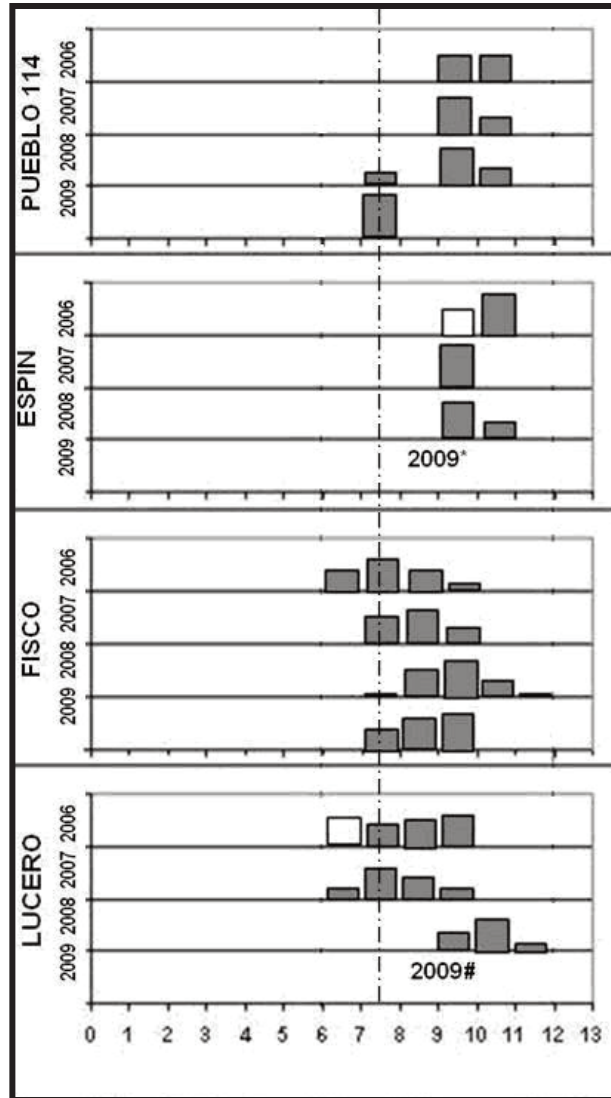


FIGURE 3. Oviposition rate of Broad-snouted Caiman (*Caiman latirostris*) in the four study sites in each year: the white bars are evidence of earlier egg deposition. The height of each bar is proportional to number of nests found in every week during the reproductive season. The x-axis represents weeks, corresponding week 1 to 2–9 November. The dotted line indicates the peak of daylight hours (21 December). *Season in which no nests were found on the site. #Season in which we could not identify the time of oviposition.

(eigenvector = 0.83), or increasing of number of days with mean temperature of 25° C (eigenvector = 0.95; Fig. 4). On the other hand, we observed a reduction in the duration of oviposition period (eigenvector = -0.82) when there was an increase in the number of days with temperatures above of 33° C (eigenvector =

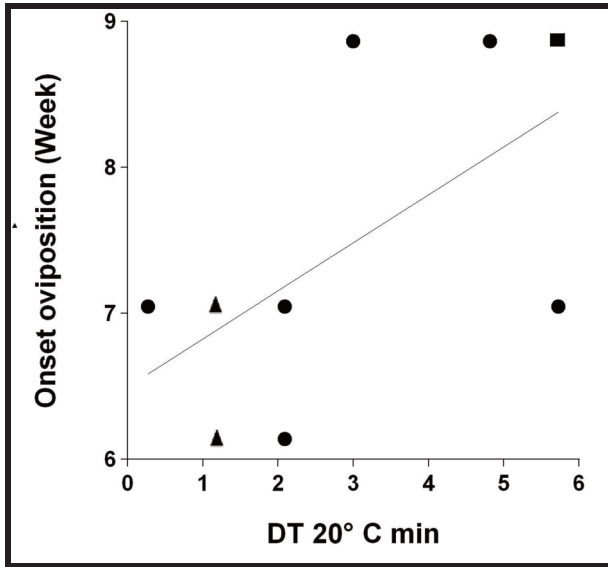


FIGURE 4. Relationship between the onset week (according to the categories assigned to each week) of the ovipositions of Broad-snouted Caiman (*Caiman latirostris*) during the breeding season, and the number of days at 20° C minimum in the previous week. Two data points in one place are represented by a triangle and a square indicated three data points in one place ($r^2 = 0.0057$; $P = 0.001$).

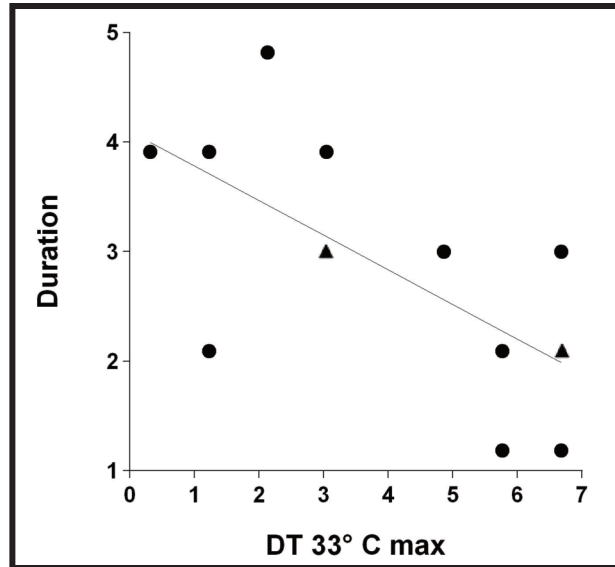


FIGURE 5. Relationship between the duration of oviposition (in weeks) of Broad-snouted Caiman (*Caiman latirostris*) during the breeding season and the number of days at 33° C maximum in the prior two weeks. Two data points in one place are represented by a triangle ($r^2 = 0.040$; $P = 0.009$).

0.84).

The week of starting oviposition for each breeding season was delayed with an increase in the number of days with temperatures below 20° C ($r^2 = 0.57$, $P = 0.001$, Fig. 5), and we found that when the number of days with temperatures above 33° C increases, the onset of oviposition was earlier ($r^2 = 0.23$, $P = 0.050$). No relationship was found between the starting week of oviposition and the number of events (storms) or the amount of rainfall in the previous week to oviposition (all $P > 0.375$). Length of the oviposition period decreased with an increase in the number of days of temperatures above 33° C ($r^2 = 0.40$, $P = 0.009$, Fig. 6). We also found that when the onset week was delayed, the duration of oviposition was shorter ($r_\rho = -0.56$, $P < 0.04$).

DISCUSSION

Oviposition timing is genetically determined in birds (Blondel et al. 1990) and lizards (Sinervo and Doughty 1996). However, it may

be also affected by biotic and abiotic factors, such as prey availability and climate (Svensson and Nilsson 1995). We found a clear relationship between environmental temperature during the previous weeks and the start of oviposition of *C. latirostris* in the southernmost distribution of the species, Santa Fe Province (Argentina) where temperature can be limiting. Additionally, there was variation in the onset of oviposition of this species in our study site. Earlier studies in *Alligator mississippiensis* found the same relationship between both variables (Joanen 1969; Joanen and McNease 1979; Kushlan and Jacobsen 1990). Therefore, it is evident that environmental temperature cannot be dismissed as a factor influencing on the life history of crocodylians (Lance 2003).

Joanen and McNease (1979) observed that oviposition timing of *A. mississippiensis* was associated with the maximum photoperiod. We found that photoperiod is not a determinant factor for the beginning of oviposition. However, we observed that 21% of females started oviposition during the week prior to maximum photoperiod (18–24 December), but most of the females (79%) laid their eggs during

a period corresponding to the four weeks after the maximum photoperiod. Our observations do not show that caiman females lay their eggs during the precise week of maximum photoperiod (week number seven), besides only five of 16 started laying on that week, indicating that maximum photoperiod is not a key factor for oviposition. Our results lead us to think that the beginning of oviposition is more likely linked to the increase in daily temperature (or decrease in days with low temperatures) rather than to increase in daylight hours. Joanen and McNease (1989) noted that when water and air temperatures increase, *A. mississippiensis* begins feeding and courtship starts. Another interesting aspect in our study is that physiognomically similar habitats somehow influence the onset of oviposition differently. For example Espin and Pueblo 114 on one side, and Fisco and Lucero on the other, showed different trends.

Conversely, to what was observed in *Crocodylus porosus*, where the oviposition period extends for three to four months (Lang 1987, 1989), *C. latirostris* in this study show a much shorter period (near three weeks). This later result is concordant to the findings in *A. mississippiensis*, *Crocodylus johnstoni*, *Crocodylus moreletti*, and *Caiman yacare* (Joanen and McNease 1989; Campos 2003; Platt et al. 2008). The duration of the oviposition period is linked to rising temperatures in both *A. mississippiensis* and *C. latirostris*, and both inhabit temperate climates with short nesting periods. By contrast, in Alligatoridae inhabiting tropical climates, the onset of oviposition is correlated with rainfall and flooding variation, such is the case of *Caiman crocodilus* in Venezuela (Thorbjarnarson 1994), *C. yacare* (Campos and Magnusson 1995), *Paleosuchus palpebrosus* (Campos and Sanaiotti 2006), and *P. trigonatus* (Magnusson et al. 1985) in Brazil, and *Melanosuchus niger* in Ecuador (Villamarín-Jurado and Suarez 2007), probably because temperature is not as variable as in temperate sites. Evidence provided in literature as well as in this study supports the idea that onset and duration of oviposition in crocodylians is related to a complex array of environmental conditions of the region they inhabit, and not linked to

phylogeny.

The variation of some environmental factors may influence the onset of reproduction, with intra and interspecific differences. However, it is still unknown what mechanisms influence this variation, especially because the relationships between environmental limitations, resource availability, and reproduction are complex (Vitt 1992; Löwenborg et al. 2010). In the present study, we found evidence of the effect of number of days with extreme temperatures on the onset of oviposition, although there may be other behavioral or physical variables affecting the dates of oviposition among females. For example, if temperature influences the development of eggs between mating and laying, the time period between mating and laying may be fixed and thus the determinant factor may be related to the mating season rather than to the oviposition period. This interaction may be also influenced by energetic quality (in terms of reserves, health status, and social hierarchic status) of females, where those females with better physical condition may nest earlier (Van Noordwijk and Jong 1986; Olsson and Shine 1997; Zera and Harshman 2001). Unfortunately, we have no information about the physical condition (size and mass) of females that laid eggs at the beginning or at the end of each breeding season. It was observed in captivity that older females of *C. porosus* produce their nests earlier in the season, laying more and larger eggs and with higher hatching survivorship (McClure and Mayer 2001). Moreover, Joanen and McNease (1992) reported the relationship of clutch size and nesting sequence, which indicated that nests containing the largest clutches are laid earliest. On other hand, under stressful conditions, crocodylians can retain eggs in the oviduct for a long period (Ferguson 1985), resulting in reduced egg viability (Wink et al. 1990). Finally, it would be interesting to determine if larger females of *C. latirostris* oviposit before smaller ones (Ferguson 1985), because neonates hatched earlier have more days with appropriated climatic conditions to feed prior to onset of the winter (in temperate climates). It should be considered that changes in oviposition timing can modify offspring phenotypic characteristics and may also affect

sex determination (Pike et al. 2006; Piña et al. 2007).

The information provided in this study would be a useful tool for the Argentinean ranching programs. Now we know that the earliest laying during the study was 12 December, and the latest was 5 January. Therefore, the job of searching for nests may be done during the last week of December and the first week of January to harvest the eggs as soon as possible after laying to reduce losses due to flooding, drought, or predation (Woodward et al. 1989). Moreover, the laying date is affected by temperature, starting earlier during warmer years. On average the laying period would be three weeks, but in cold years (when the onset of laying is later) it will be reduced.

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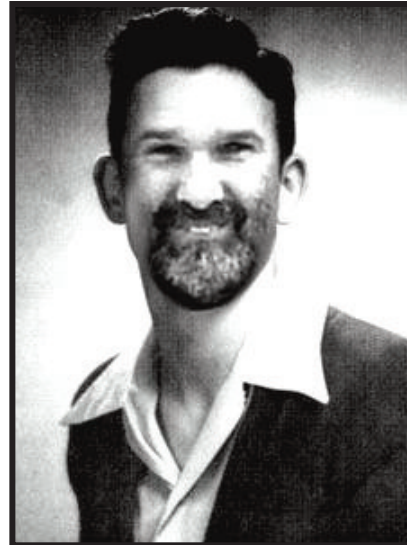
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