PREVALENCE AND DETAILS OF POLYDACTYLISM IN THE AMERICAN Alligator, *Alligator mississippiensis*, in Louisiana, USA

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Abstract.—Polydactylism has been described in the American Alligator (*Alligator mississippiensis*) and other crocodilians, but to our knowledge the prevalence of this limb abnormality has not been examined in detail. As part of a head start program in which juvenile alligators are released back to the wild after being hatched from eggs collected in the wild, in 2016 we examined 58,106 alligators for this condition. Polydactylism occurred in 106 alligators (0.18%). Front limbs and limbs on the right side were more commonly affected than rear limbs or those on the left side (n = 77 right front and n = 59 left front; n = 34 right rear and n = 20 left rear). Of the 106 alligators with polydactylism, extra toes were present on one limb in 46 cases (43.40%), on two limbs in 42 instances (39.62%), on three limbs in 12 alligators (11.32%) and six alligators had extra toes on all four limbs (5.66%). Analyses of patterns of polydactylism could not support hypotheses that polydactylism was more common on any combination of position (front, back, left, right) based on number of limbs affected. Alligators typically have 18 toes; the mean number of toes present in this series of polydactylism was $22.5 \pm$ (SD) 2.8 toes (range 19–32). One alligator had eight toes on each limb, for a total of 32 toes present (14 more than normal). Several other cases of polydactylism were noted in review of anecdotal observations recorded from farm releases made in prior years, from hatchlings obtained from eggs collected and incubated at Rockefeller Wildlife Refuge in Grand Chenier, Louisiana, or from wild harvested alligators taken in statewide sanctioned harvests.

Key Words.-extra digits; limb abnormalities; polydactylism; toes

INTRODUCTION

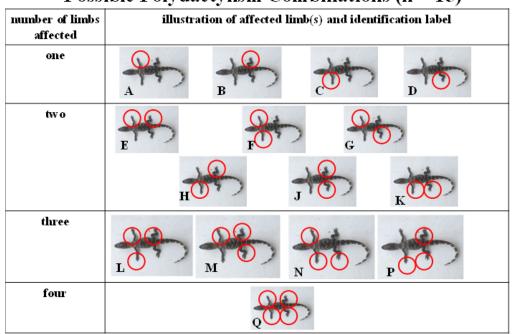
American Alligators (Alligator mississippiensis, hereafter Alligator) normally have five toes on the front feet and four toes on the hind feet (Giles 1948). Polydactylism (presence of extra digits) has been described in a wild juvenile Alligator (Giles 1948) as well as embryonic alligators (Ferguson 1981, 1982, 1985). Other crocodilians have also been reported to exhibit polydactylism, including Crocodylus porosus (Saltwater Crocodile; Deraniyagala 1936), C. johnstoni (Australian Freshwater Crocodile; Ferguson 1985), C. niloticus (Nile Crocodile; Huchzermeyer 2003), and other Crocodylus sp. (Youngprapakorn et al. 1994) as noted in Charruau and Nino-Torres (2014). Other skeletal malformations such as presence of extra limbs, absent digits or limbs, and syndactylism have been reported in crocodilians, including alligators (see reviews by Ferguson 1985 and Charruau and Nino-Torres 2014).

The Louisiana Department of Wildlife and Fisheries (LDWF) in the USA manage the alligator as a renewable natural resource. One aspect of the management program is an alligator egg ranching program, whereby licensed alligator farmers are permitted to collect

conservative quotas of eggs from wild alligator nests. To ensure future population recruitment, a portion of the hatchlings produced from ranched eggs must be released back to the wetland from which the eggs were collected within two years of hatching, at which point the alligators are large juveniles. These head start alligators are between 91.4 and 152.4 cm (36–60 in) total length (TL) at release. Due to the large quantities of eggs collected in Louisiana (over 500,000 eggs in peak years), 40,000–50,000 or more juvenile alligators are released in some years. The alligator release program is described in detail by Elsey and Kinler (2011).

Because LDWF staff examine and handle each alligator to be released back to the wild, we had the opportunity to survey a large quantity of captive-raised alligators to determine prevalence of polydactylism in alligators. Additional objectives of this study were to determine which limbs were most commonly affected by polydactylism (front limbs vs. hind limbs; right limbs vs. left limbs) and if any patterns of affected limbs were more common (affected limbs both on the same side of the body [ipsilateral] vs. limbs on opposite sides of the body involved [contralateral]). Additionally, we reviewed and summarized previous anecdotal accounts of polydactylism in captive (farm-raised) and wild

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Possible Polydactylism Combinations (n = 15)

FIGURE 1. Patterns of polydactylism in American Alligators (Alligator mississippiensis) from Louisiana, USA, identified by which limbs were affected.

alligators encountered during other research studies or the annual sanctioned fall harvest in Louisiana, USA.

MATERIALS AND METHODS

Personnel of the LDWF travel to alligator farms statewide to conduct releases of farm raised juvenile alligators back to the wetlands from which the eggs had been collected one or two years earlier. Although a few producers maintain adult alligators for captive breeding propagation, it is generally more economical for most facilities to collect eggs from the wild (egg ranching), and hatchlings obtained from closed cycle captive breeding is very low (1.1% of the 2014 hatchling stock, and 1.9% of the 2015 hatchling stock). Thus, although the alligators provided for release to the wild are reared in captivity, almost all originated from eggs collected in the wild. The releases are made during spring and summer to enhance survival, with legal dates to schedule releases to the wild being from 15 March to 25 August each year. At farm sites, LDWF staff measure TL of each alligator to be released to the nearest 2.54 cm (1 in), notch the tail for permanent identification, determine the sex by opening the cloaca with a nasal speculum to evaluate the genital morphology (Allsteadt and Lang 1995), and place numbered monel web tags in the webbing between the toes of each rear foot (additional details on the release procedure are in Elsey and Kinler 2011). The alligators are then placed in burlap bags for transport to the wetlands from which alligator eggs had been collected. If polydactylism was observed, the identifying web tag of that alligator was noted, as well as the quantity of toes on each limb. All alligators examined for this study were processed between 15 March and 25 August 2016.

Alligators presented for release to the wild are generally selected based on hide quality. Farmers receive higher prices for their best quality alligator hides, and thus they carefully inspect the hides of alligators before selecting those destined for sale to the luxury leather goods markets. Those with minor imperfections on the hide might be used for release to the wild. Unhealthy alligators and alligators with abnormalities, such as partial tail amputations (bob-tails) or jaw malformations that might preclude normal feeding, are not accepted for release to the wild. Fifteen patterns or combinations of limbs affected by polydactylism are possible (Fig. We categorized each instance of polydactylism 1). identified during farm releases by the pattern of limbs affected.

In 2016, releases were conducted on 72 d within the allocated time frame. Typically we worked one alligator farm site each day, but on some days we made releases at more than one farm facility if the release quantities were small and the farms were in close proximity. We made releases at 17 farms, and on a typical day, we tagged approximately 750–1,000 alligators for release. In 2016 the quantity of alligators released by individual farmers ranged from 10 to 1,231 alligators on any given day. Five farmers released alligators only once in 2016,

TABLE 1. Patterns of polydactylism identified in 106 juvenile American Alligators (*Alligator mississippiensis*) from wild collected eggs, then reared on alligator farms in 2016 in Louisiana, USA. Abbreviations are NLA = number of limbs affected, PD = pattern designation, QP = quantity of that pattern, and PP = percentage of that pattern.

NLAPDQPPPWhich Limb(s) AffectedOneA2220.75right frontB1312.26right rearC87.55left frontD32.83left rearTotal4643.40TwoE43.77F3533.02right front, right rearG00right front, left frontJ32.83right rear, left frontG00right rear, left frontJ32.83right rear, left frontJ32.83right rear, left frontJ32.83right rear, left rearH00left front, left rearTotal4239.62ThreeL43.77N43.77right front, right rear, left frontM21.89right front, left rearP21.89right front, left front, left rearTotal1211.32FourQ65.66Total65.66					
B 13 12.26 right rear C 8 7.55 left front D 3 2.83 left rear Total 46 43.40	NLA	PD	QP	PP	Which Limb(s) Affected
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	Total		6	5.66	

other farmers required multiple release days (up to 16 d) to fulfill their obligations for eggs collected previously.

For statistical analyses of 2016 farm data, we counted selected occurrence(s) of polydactylism and number of limbs affected, although proportions of occurrences offered an alternative analysis path (i.e., beta regression). Because the large number of zeros in the dataset can be addressed with zero inflated generalized linear models, counts presented robust analytical options with zero-inflated generalized linear models. Thus, the response variable in the data analysis was the count of occurrences of explanatory variables (e.g., 22 alligators had one right front limb affected and four alligators had a right front and right rear leg affected; therefore, the response is 22 for the first combination and four for the second combination). For comparisons of polydactalism by limb position (front, back, right, left) and number of affected limbs, we used two zero-inflated generalized linear models (Poisson and negative binomial alternatives) to test for changes in the aforementioned counts related to the fixed explanatory variables of position and number of affected limbs. In this implementation of zero-inflated generalized linear model, models evaluated one explanatory variable at a time to determine whether the explanatory variable was influential on the presence of polydactylism, termed the zero-inflation variable, and the other explanatory variable assessed the changes in counts. For testing the effect of position on the counts of polydactylism, the number of limbs affected served as the zero inflation variable, and for testing the number of affected limbs on the counts of polydactylism, positions served as the zero inflation variable. We used a \hat{c} (Pearson χ^2 / degree of freedom fit statistic) closer to 1 to determine the choice of Poisson or negative binomial versions of the model selected for inference. We set statistical significance at $\alpha = 0.05$ and we performed all analyses in SAS/STAT (vers. 9.4, SAS Institute, Inc., Cary, North Carolina, USA).

RESULTS

In 2016 we tagged 58,106 farm alligators for release to the wild, of which 106 (0.18%) had polydactylism. Of the 72 release days, we observed at least one alligator with polydactylism on 41 d (56.94%). The most alligators seen with polydactylism on a given day was seven of the 595 alligators tagged that day (1.18%).

The mean total length of alligators with polydactylism was $117.1 \pm (SD) 13.8 \text{ cm}$ (range 91.4-152.4 cm; n = 104; length unknown for two alligators). The sex ratio for polydactyl alligators observed was 65.1% females, 33.0% males, and 1.9% sex unknown. The affected population was demographically similar to the released population suggesting against a sex bias. The sex ratio for all 58,106 alligators released was comparable at 60.1% females and 39.9% males, and average size was 122.1 cm TL.

Alligators typically have 18 toes (Giles 1948; Ferguson 1981) and the mean number of toes present in this series of polydactylism was 22.5 ± 2.8 toes (range 19-32, n = 106). One alligator had eight toes on each limb, for a total of 32 toes present (14 more than the normal). Of the 106 alligators with polydactylism, extra toes were present on one limb in 46 cases (43.40%), on two limbs in 42 instances (39.62%), on three limbs in 12 alligators (11.32%) and on all four limbs in six alligators (5.66%). We assigned an alphabet letter for the pattern of affected limbs (Fig. 1). The most common configuration (33.02%) of toes we observed was pattern F, wherein both front limbs had extra toes (Table 1). The next most frequent pattern we observed was an affected right front limb (20.75%), followed by an affected right rear limb (12.26%). Three possible patterns were not observed (G, H, and K; Table 1). Of the four limbs, the right front limb was most commonly affected (n = 77), followed by the left front (n = 59), the right rear (n = 34)and the left rear limb (n = 20).

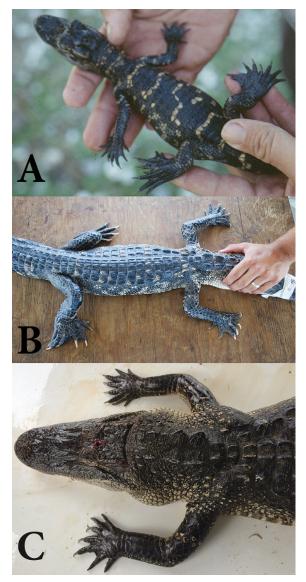


FIGURE 2. Polydactylism in American Alligators, *Alligator mississippiensis*, from Louisiana, USA. (A) hatchling, pattern Q. (B) juvenile 132.1 cm total length (TL), pattern L. (C) adult 223.5 cm TL, pattern F. (Photographed by Ruth M. Elsey).

When two limbs were affected, contralateral limbs were involved more often (35 cases of pattern F, three cases of pattern J, no cases of patterns G or H) than an ipsilateral distribution (four cases of pattern E, no instances of pattern K). Affected alligators more often had more than two additional toes, rather than only one or two additional toes. For example, eight toes were present on the right front, right rear, left front, and left rear limbs 47, 12, 35, and eight times, respectively. Seven toes occurred on these limbs only 13, seven, 14, and four times; while six toes were present on those limbs 17, nine, 10, and seven times, respectively.

We noted several other cases of polydactylism when we reviewed anecdotal observations recorded from three sources, including: farm releases made in prior years, hatchlings obtained from eggs collected from the wild and incubated at Rockefeller Wildlife Refuge in Grand Chenier, Louisiana, USA, and wild harvested alligators taken in statewide sanctioned harvests (Table 2, Fig. 2). For both analysis of position and number of limbs, the best fitting zero-inflated general linear model was the negative binomial version. The model did not detect a statistically significant difference in polydactylism by limb position suggesting insufficient evidence for selection of polydactylism and in favor of a stochastic process ($\chi^2 = 3.24$, P = 0.070). Similarly, no statistically significant patterns were detected for the number of limbs affected ($\chi^2 = 2.19$, P = 0.140). It is worth noting that the overall sample size was modest and polydactylisms were relatively few, therefore, it is possible that with additional samples, statistically detectable patterns in position and number of polydactylisms could emerge.

DISCUSSION

To our knowledge, this study is the first large-scale survey to determine prevalence of polydactylism in a crocodilian. Although uncommon, we documented 106 cases from 58,106 alligators (0.18%). Because LDWF staff often tags 1,000 or more alligators in a day and generally can process the alligators in a rapid assembly line method, it is possible to measure, tail notch, web tag, determine the sex, and bag up to 300 alligators per hour under optimum conditions. Thus, it is possible that some alligators with polydactylism may have been overlooked, particularly if it occurred on the front limbs. Web tags are placed in the webbing between the toes of each rear limb, so it would be unlikely to overlook polydactylism present in the rear limbs. Thus, polydactylism may occur at slightly higher levels than reported here, although staff conducting the work to process each alligator were instructed to carefully inspect each alligator for polydactylism. Similarly, in a large series of wild alligators collected for research (Lance et al. 2015) we noted only one case of polydactylism; however, for that project team members were not asked to look for nor record polydactylism, which could have easily occurred more often and been overlooked as collection efforts were conducted mostly at night. One of the five cases of polydactylism noted from wild adult alligators captured during sanctioned harvests had extra toes on the right rear and left front limb (pattern H); this pattern was not seen in the 106 farm released alligators with polydactylism in this series.

Numerous causes of congenital deformities in crocodilians have been discussed and include such

Date	Total Length (cm)	Pattern	Remarks/Source
December 1994	hatchling	Q	Rockefeller Refuge, from wild collected egg
February 1996	juvenile approx. 61 cm	Q	Rockefeller Refuge, from wild collected egg
August 1991	juvenile approx. 91 cm	J	ranched farm release to the wild
September 1991	juvenile approx. 107 cm	L	ranched farm release to the wild
6 August 2009	109.2	В	ranched farm release to the wild
21 August 2009	118.1	Е	ranched farm release to the wild
3 August 2009	129.5	В	ranched farm release to the wild
9 July 2009	132.1	L	ranched farm release to the wild
3 August 2009	132.1	L	ranched farm release to the wild
21 July 2009	137.2	В	ranched farm release to the wild
21 July 2009	142.2	F	ranched farm release to the wild
11 December 2000	236.2	С	Rockefeller Refuge, wild research alligator
September; year unknown	264.2	B or D	wild alligator, sanctioned harvest
September 2013	adult	С	wild alligator, sanctioned harvest
5 September 2014	adult	Н	wild alligator, sanctioned harvest
11 September 2015	223.5	F	wild alligator, sanctioned harvest
10 September 2016	adult approx. 213 cm	А	wild alligator, sanctioned harvest

 TABLE 2. Additional cases and patterns of polydactylism in American Alligators (*Alligator mississippiensis*) in Louisiana, USA. Note the juvenile from February 1996 may be the same alligator as the December 1994 hatchling.

factors as extremes in age or poor nutrition of the mother, sub-optimum embryo incubation conditions at the limits of viable incubation range, exposure to teratogens, or genetic causes (Ferguson 1982, 1985, 1989; Webb and Cooper-Preston 1989; Charruau and Nino-Torres 2014). Abnormalities in anuran limbs have also been attributed to trauma, mutations, predation, parasites, hybridization, or exposure to UV radiation or chemical contaminants (Lannoo 2008); these malformations might be indicators of ecosystem disruption (Sousa and Costa-Campos 2016). However, it has been reported that UV exposure more often involves missing or reduced (rather than duplicated) digits in anurans (Ankley et al. 2000). Limb malformations in amphibians may occur as a result of environmental contamination by pesticides or fertilizers (Sparling et al. 2015, as noted in Monico et al. 2016). To our knowledge there were no environmental contaminant concerns in wetlands from which the alligator eggs in this study were collected (Lance 2008). Indeed a record high alligator nest production occurred in 2016 (estimated 58,100 nests surveyed in coastal Louisiana; LDWF, unpubl. data) indicating overall healthy marsh conditions. Licensed egg collectors harvested 616,546 alligator eggs in Louisiana in 2016, and hatched a record 88.9%, which indicates health of the embryos as well. It is unknown if survival of embryos or hatchlings with polydactylism is different from those without this condition, but this would be an area for future study.

In a study of cleft palate in embryonic alligators, Ferguson (1981, 1982) administered teratogens at varying times in development, and in some cases induced production of polydactylism as well. Teratogens to which alligator embryos were exposed included 5-fluoro-2-desoxyuridine (FUDR) and hydrocortisone. He also reported that hatchlings emerging from eggs incubated at higher temperatures (above 34° C) frequently exhibited extra digits (Ferguson 1982). In a small study of three alligator nests in Texas from which 101 hatchlings were obtained, an unspecified number (listed as several) had extra digits (Crouch 1977). This study site was a reservoir that received thermal effluents, with a discharge canal containing warmer water than surrounding habitat. The author did not report alligator nest temperatures. It is possible the thermal effluents and warmer canal water may have affected the reproductive physiology of nesting females and led to the very high rate of polydactylism; however, the unusually long incubation periods in that study due to heavy rainfall (Crouch 1977) suggest perhaps lower than optimum nest temperatures may have been a causative factor. Cooler temperatures slow embryonic development in alligators (Lang and Andrews 1994), thus the long incubation times Crouch observed might indicate nest temperatures were unusually low. In humans, polydactylism can occur by itself (typically an autosomal dominant mutation) or in association with other congenital abnormalities (Kapoor and Johnson 2011). In this series, no other abnormalities were noted on the 106 farm raised alligators with polydactylism.

Although this paper describes polydactylism in alligators tagged and released from Louisiana alligator farms, it is possible this condition occurs in Alligators in other southeastern states. It is legal for Louisiana alligator farmers to import live alligators from licensed alligator farms in other southeastern states to add to their farm inventory. In 2014, 14.4% of the hatchling stock on Louisiana farms was imported from Florida and Texas, and in 2015, 16.8% of the 2015 year class had been imported from the same states. Thus, it is possible that some of the alligators with polydactylism herein described may have originated in states other than Louisiana, as hatchlings from the 2014 and 2015 year classes would have been of the appropriate size/ age for releases conducted in 2016. However, of the 11 farm facilities from which we observed polydactylism in alligators in 2016, only six had imported alligators from out of state in 2014, and only four did so in 2015. Thus, the majority of the polydactyl alligators in this study originated from Louisiana, but a few may have originated from Florida or Texas.

The alligator has been used as a model to study digit reduction in archosaurs (Larsson et al. 2010). Additionally, alligator tracks can be used to estimate body size, and measurement error is minimal as track length differs little from the actual rear foot length (Platt et al. 1990; Wilkinson and Rice 2000). This relationship has also been used to estimate size of nesting female alligators from tracks measured at nest sites (Platt et al. 1995). Crocodilian tracks can be useful in a variety of field studies (Platt et al. 2014), as rear track length measurements can be a reliable estimator of total length in numerous crocodilian species (Platt et al. 2009, 2011). A recent study described footprints and trackways of wild alligators and how they relate to the direction of travel in a walking alligator; similar studies may be important to palichnologists interpreting fossil crocodilian tracks (Farlow and Elsey 2010). Simpson (2006) characterized the rear-foot tracks of crocodilians with the imprint of four toes and webbing. Of note, a rear footprint of a crocodilian with polydactylism (particularly if five toes occur on the affected rear foot) could be misinterpreted as a front foot print leading to erroneous size estimates, as the forefeet are much smaller (Hutton 1987) and crocodilians support more body weight on their hindlimbs than on their forelimbs (Allen et al. 2010). Because polydactylism is rare, it is unlikely to occur and be misinterpreted in field situations as per above, but it is a possibility scientists might need to consider if distorted or abnormal footprints/tracks are observed.

In summary, polydactylism occurs in many varied patterns in *A. mississippiensis*, both in wild alligators and in captive reared specimens obtained from eggs collected from the wild. Huchzermeyer (2003) reported polydactylism usually has no deleterious effect on the functioning of the limbs in crocodilians. Fortunately this would suggest there is no adverse impact by presence

of this condition to conservation or management of crocodilian species. Similar to Huchzermeyer (2003), we also saw no problems with locomotion or swimming performance during casual observations in the few instances wherein we maintained polydactyl alligators in captivity at Rockefeller Refuge. It would be of interest to evaluate gait and swimming performance in detail in crocodilians with polydactylism to determine if the extra digits provide additional thrust while swimming, or if additional drag or water resistance might be an impediment to streamlined mobility. Additionally, if a nesting female crocodilian exhibited polydactylism, it might be possible to evaluate a possible genetic cause of this condition, if hatchlings from that female had limb or digit abnormalities.

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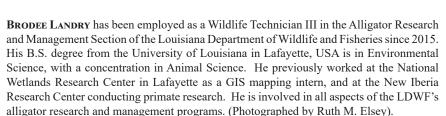
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alligators in Louisiana. (Photographed by Ruth M. Elsey).

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