Patterns of temporal variation in growth rate from a mainland population of *Anolis nebulosus* (Squamata: Dactyloidae), in the Mexican Pacific Coast

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In this study we used three nonlinear regression models: Von Bertalanffy, logistic-by-length, and logistic-by-weight to describe the pattern of growth of hatchling, juvenile, and adult of the lizard *Anolis nebulosus* in a tropical dry forest near of the Mexican Pacific coast during a period of 1989 and 1990. Von Bertalanffy and logistic-by-length models showed the best fit to the growth data for males and females of three age classes from marked and recaptured lizards in these years. The characteristic parameter of growth (r) and asymptotic growth (A_1) extracted from these models indicated that males grow faster than females, but the latter reach a slightly larger size than males. The growth curves revealed that males reach minimum size at sexual maturity at 35 mm in snout-vent length (SVL), at an age of seven months, while females reach sexual maturity at 37 mm of SVL at nine months. Comparisons of growth rate between wet and dry seasons and years revealed that hatchlings and juveniles of both sexes had higher growth during the wet season for both years. Although there was no significant variation between measured environmental variables or in the food availability, the weight of evidence suggests that environmental variation has an influence on the growth of *A. nebulosus* of this population. Results indicate that variation on growth patterns observed may result from a combination of environmental factors, such as food availability, predation pressure and some reproductive characteristics as size at sexual maturity and size of hatchlings at birth.

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23   ABSTRACT

24   In this study we used three nonlinear regression models: Von Bertalanffy, logistic-by-

25   length, and logistic-by-weight to describe the pattern of growth of hatchling, juvenile, and

26   adult of the lizard *Anolis nebulosus* in a tropical dry forest near of the Mexican Pacific

27   coast during a period of 1989 and 1990. Von Bertalanffy and logistic-by-length models

28   showed the best fit to the growth data for males and females of three age classes from

29   marked and recaptured lizards in these years. The characteristic parameter of growth (r) and

30   asymptotic growth (A_1) extracted from these models indicated that males grow faster than

31   females, but the latter reach a slightly larger size than males. The growth curves revealed

32   that males reach minimum size at sexual maturity at 35 mm in snout-vent length (SVL), at

33   an age of seven months, while females reach sexual maturity at 37 mm of SVL at nine

34   months. Comparisons of growth rate between wet and dry seasons and years revealed that

35   hatchlings and juveniles of both sexes had higher growth during the wet season for both

36   years. Although there was no significant variation between measured environmental

37   variables or in the food availability, the weight of evidence suggests that environmental

38   variation has an influence on the growth of *A. nebulosus* of this population. Results indicate

39   that variation on growth patterns observed may result from a combination of environmental

40   factors, such as food availability, predation pressure and some reproductive characteristics

41   as size at sexual maturity and size of hatchlings at birth.

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43   Keywords. capture-recapture, growth rate, lizard, sexual maturity, Von Bertalanffy model,

44   Chamela, Jalisco.

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46   INTRODUCTION

47   Tinkle (1969) predicted life history patterns in lizards that fall along a continuum with two

48   extremes. The first pattern comprises short-lived, small species, with rapid growth rates,

49   early maturity, and multiple clutches/yr; it includes oviparous, tropical species in which

50   natural selection favors high reproductive effort. The second pattern comprises long-lived

51   species that grow slowly, show large body size, late maturity, and a single larger clutch per

52   reproductive season; it includes viviparous and oviparous species from temperate and

53   tropical environments where natural selection favors low reproductive effort (Tinkle, 1969;

54   Tinkle, Wilbur & Tilley, 1970; Stearns, 1992). Based on these predictions, many studies

55   have confirmed variation in growth patterns in lizard species from tropical (Andrews, 1976;

56   Ramírez-Bautista, 1995) and temperate environments (Dunham, 1978; Ballinger &

57   Congdon, 1980; Pérez-Mendoza & Zúñiga-Vega, 2014), which are related to age and size

58   at sexual maturity, fecundity/fitness (Charnov & Berrigan, 1991), and survival rate (Ogutu

59   & Owen-Smith, 2006; Pérez-Mendoza & Zúñiga-Vega, 2014).

60   Within these life history patterns in lizards, growth rate has been studied from two

61   major perspectives: ecological and phylogenetic (Zamora-Abrego, Zúñiga-Vega & Ortega-

62   León, 2012). The ecological approach considers body growth rate as an expression of food

63   availability, environmental factors (temperature and precipitation), parasitism and foraging

64   (Adolph & Porter, 1996; Bronikowski, 2000; Kratochvil & Frynta, 2003; Pérez-Mendoza &

65   Zúñiga-Vega, 2014), whereas the phylogenetic perspective considers evolutionary history

66   as the primary factor in explaining variation in life history characteristics (age at maturity,

67   fecundity, survival) among related or unrelated species (Dunham, 1978; Sinervo & Adolph,

68   1994).

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69   Of the 391 species currently described within the genus *Anolis*, about 30 species

70   show small body size and rapid growth (Dunham, 1978; Andrews, 1979; Ramírez-Bautista,

71   1995), while the rest of species are large or medium-sized and show slower growth rates,

72   among other differences such as survival, reproduction and diet (Sinervo, 1990; Sinervo &

73   Adolph, 1994). Additionally, it also has been discussed that growth rate among species and

74   populations is related to sex, for example, in many cases males grow faster than females

75   due to they need to reach sexual maturity faster to mate and begin to reproduce (Ramírez-

76   Bautista, 1995; Webb, Brook, Shine, 2003; Pérez-Mendoza & Zúñiga-Vega, 2014).

77   In populations of lizards of the genus *Anolis* from island and mainland

78   environments, environmental factors may influence life history traits such as growth rates

79   (Zúñiga-Vega et al., 2005). For example, the availability of food was a primary regulator of

80   growth in two populations (island and mainland) of *A. oculatus* and *A. limifrons*, where

81   according to the authors, males and females of the islands present slow growth rates and

82   mature to a larger size. This was explained by the hypothesis that there is less food on the

83   island than in the continent (Andrews, 1976). Schoener & Schoener (1978) found in four

84   lizard species of the genus *Anolis* that growth rate was lower in females than males,

85   because their observations suggested that females fed for a shorter time than males, due to

86   several groups of adult males monopolizing the food and foraging places during both wet

87   and dry seasons. In *A. carolinensis*, Goodman (2010) found individuals from northern

88   populations were larger and exhibited higher growth rates than those from the south,

89   suggesting that individuals from the north are able to store more energy as adults to help

90   withstand the lower temperatures of the winter months (Michaud & Echternacht, 1995).

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91   In this study, we assessed temporal variation in growth rates of adults, juveniles and

92   hatchlings of both sexes of *A. nebulosus* as a function of temperature, precipitation and

93   food availability. We estimated lizard growth rates using the standard growth rate (r) as

94   well as asymptotic growth rate (A_1). Thus, the goals of this study are (1) determine whether

95   there are differences in growth rate among age classes and between sexes and years of *A.*

96   *nebulosus*, (2) determine the age at sexual maturity for each sex, and (3) document

97   variation between wet and dry seasons and years in the growth rate among age classes of

98   this species living in a seasonal tropical environment of the Chamela region from the

99   Pacific coast of Mexico.

100   Due to ecological approach as influence of environmental on life history traits or

101   growth rates (Zúñiga-Vega et al., 2005), we expected that growth rates of different age

102   classes and sexes of *A. nebulosus* would be higher during the wet season than the dry

103   season in response to a greater availability of insects in the environment during the wet

104   season (Andrews, 1979; Ramírez-Bautista, 1995).

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106   MATERIALS AND METHODS

107   Study area and field work

108   This study was carried out at the Estación de Biología Chamela (EBCH), located between

109   the towns of Chamela and Careyes, Jalisco, Mexico (19°31´31.8´´N, 105°03´44.5´´W,

110   Datum WGS 84), 2 km from the Pacific coast at an elevation of 125 m. The vegetation

111   type is tropical dry forest, with patches of deciduous forest and desert scrub (Trejo-

112   Vázquez, 1988).

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113   Sampling was conducted from June 1988 to December 1991 for 10 days each month for a

114   total of 43 sampling periods (Ramírez-Bautista, 1995). Most individuals, however, were

115   captured, marked, and recaptured during 1989 and 1990; therefore, growth analyses are

116   derived only from those two years of sampling. Because *A. nebulosus* is arboreal, lizards

117   were encountered in 165 trees along a 1,000 m x 10 m transect; 708 lizards (351 males, 357

118   females) were captured and marked by toe-clipping. Toe-clipping method has been the

119   most used to follow the cohort of a lizard population (Dunham, 1978; Tinkle, 1960, Tinkle

120   et al., 1970). Lately, Guimaraes et al. (2014) and Olivera-Tlahuel et al. (2017) have pointed

121   out to pay more attention in using this method because they observed effects on the

122   behavior and health of some lizard species, and therefore, survival. However, during our

123   study was tested that this method (Toe-clipping) does not affect the behavior and survival

124   of the marked individuals, which was reflected in the capture and recapture lizards

125   (Ramírez-Bautista & Vitt, 1998; Hernández-Salinas et al., 2014). Also, in future studies it

126   is necessary development different methods to follow a cohort of these species. The field

127   work in which data from this project was obtained, was authorized by the normativities of

128   Guidelines for the Care and Use of Lower Vertebrates (1986), the national normativities

129   CT-CERN-001-91 (DOF, 1991) and NOM-PA-CRN-001/93 (DOF, 1993), and the intern

130   reglement of Estación de Biología Chamela, UNAM.

131   We recorded a total of 1,568 capture-recapture events, ranging from once up to 12 times.

132   For each capture, we measured snout-vent length (SVL mm; nearest 0.01 mm using

133   calipers), weight to the nearest 0.1 g using a 10-g Pesola scale, sex (based on presence or

134   absence of a conspicuous dewlap, present only in males), and presence of a complete or

135   regenerated tail (Ramírez-Bautista, 1995). After these data were recorded, lizards were

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136   returned and released at their initial capture location. Sampling was performed between

137   0800 to 1900 h, which was within the daily activity period of *A. nebulosus* (Ramírez-

138   Bautista, 1995; Ramírez-Bautista & Vitt, 1997).

139

140   Growth model

141   Marked lizards comprise 3 different age classes: hatchlings, juveniles and adults. Male and

142   female individuals were considered adults when they had a SVL minimum of 32.0 and up

143   to 50.0 mm and 35.0 to 40.0 mm, respectively. Juvenile individuals were considered with a

144   SVL from 25.0 to 31.0 mm to male, and from 25.0 to 34.0 mm to female. Finally,

145   individuals with a SVL from 19.0 to 24.0 mm were grouped as hatchlings (Ramírez-

146   Bautista, 1995).

147   Growth rate for captured-recaptured individuals at different age classes (hatchlings,

148   juveniles and adults) was described with the equation: $GR = (SVL_2 - SVL_1) / day$. Where

149   growth rate (GR) is the difference between SVL of the last recapture event (SVL_2) and the

150   first one (SVL_1) divided by the number of days elapsed between them (Dunham, 1978;

151   Zamora-Abrego, Zúñiga-Vega & Ortega-León, 2012).

152   Growth rate was recorded over recapture intervals of > 30 days and < 100 days.

153   Growth data, assessed by age class, sex and year were then subjected to three nonlinear

154   regression models: the Von Bertalanffy model, the logistic-by-length model and the

155   logistic-by-weight model (Dunham, 1978; Schoener and Schoener, 1978). The first model

156   provides a relationship among sizes of the individuals and their growth rate (Dunham,

157   1978; Zamora-Abrego, Zúñiga-Vega & Ortega-León, 2012; Table 1). This relationship

158   assumes that smaller individuals have faster growth rates than larger ones (Dunham, 1978;

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159 Zamora-Abrego, Zúñiga-Vega & Ortega-León, 2012). On the other hand, the logistic-by-

160 length and logistic-by-weight models predict that small individuals will grow moderately

161 fast as they reaching intermediate sizes; once growth rate is maximized it will decrease

162 nonlinearly with increasing size (Dunham, 1978; Schoener & Schoener, 1978; Zamora-

163 Abrego, Zúñiga-Vega & Ortega-León, 2012; Table 1). The difference between these latter

164 two models is that the maximum growth rate is reached at an earlier age in the logistic-by-

165 length model, whereas the logistic-by-weight model predicts that maximum growth rate is

166 reached at a later age (Dunham, 1978). The details of the differential description of each

167 model can be reviewed in Dunham (1978) and Schoener & Schoener (1978). The choice of

168 the best model was based over the best fit of growth rate for age class, sex and year

169 (together), chosen by the lowest values of the residuals error mean square (MSR) and the

170 highest coefficient of determination or correlation (R^2; Dunham, 1978; Schoener &

171 Schoener, 1978).

172   Once best models were identified, we elaborated confidence intervals for growth

173 parameters (r, or characteristic growth rate) and (A_1 the asymptotic body size) under the

174 following formula (Schoener & Schoener, 1978):

175 $\theta_j - \sqrt{kF_{1-\alpha\ (k,\ N-K)}}\ S_j^2 \leq \beta_j \leq \theta_j + \sqrt{kF_{1-\alpha\ (k,\ N-K)}}\ S_j^2$

176 where β_j is the adjusted parameter j, θ_j is the estimate of β_j, S_j is the asymptotic standard

177 deviation of β_j, $F_{1-\alpha}^{(k,N-k)}$ is the 1-tailed value of $F_{1-\alpha}$ with k and $N - k$ degrees of

178 freedom, N is the sample size and k is the number of adjusted parameters.

179   Based on the solution of the best model data were used to build growth curves for

180 both males and females using the average of size at birth (L_0) of male and female hatchlings

181 ($\overline{X}$ = 22.06 ± 1.5 mm, 19.0-24.0 mm, n = 22). With this curve we were able to estimate the

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182   age at sexual maturity for each sex (Dunham, 1978; Schoener & Schoener, 1978; Zamora-

183   Abrego, Zúñiga-Vega & Ortega-León, 2012). We used a two-way ANOVA to identify any

184   differences in growth rate of age classes and sex, using season (wet and dry), and year as

185   the factors, and as response variable to the residuals from the model of growth with the best

186   fit, which are the result of the analysis of nonlinear regression between body growth rates

187   and SVL for each individual (Zamora-Abrego, Zúñiga-Vega & Ortega-León, 2012).

188   To assess the availability of prey in the environment, insects were collected by the

189   trawl net method, which consists of a trawl with a cylindrical aluminum ring 40 cm in

190   diameter attached to a wooden stick 120 cm long. Using this trawl net, we applied 20

191   strokes on three different sites chosen at random along the transect where the lizards were

192   captured and released. These sites were spaced 100 m from each other. Insects were

193   sampled several times per month: on the first, the seventh, and one day before the end of

194   field activities for that month. This enabled us to obtain a representative sample of insect

195   abundance in the study area (Ramírez-Bautista, 1995). Insects collected were euthanized by

196   freezing, preserved in 70% alcohol, and subsequently identified by the senior author (ARB)

197   to the level of order. Results were corroborated using keys of Triplehorn & Johnson (2005).

198   We regarded different insect orders as prey categories. Additionally, prey in the orders

199   Coleoptera, Hymenoptera and Lepidoptera were categorized as larvae or adult stages. To

200   develop comparisons between the number of categories and number of individuals of each

201   prey between season (wet and dry) and years, we used a Student *t* test for independent

202   samples (Zar, 1999). We applied Pearson correlations to test for a possible relationship

203   between growth rates with environmental variables temperature and precipitation, and the

204   number of prey categories and number of insects in the environment, considering

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205   environmental variables and insects as independent and growth rates as dependent (Adolph

206   & Porter, 1996). Temperature and precipitation data were taken from the Meteorological

207   Station of the EBCH, Universidad Nacional Autónoma de Mexico (UNAM) during the

208   fieldwork. Estimations of growth rate were obtained using the software Statistica 7.0.

209   Means are given ±1 S.E. unless otherwise indicated and with a significance level of 0.05

210   (Zar, 1999).

211

212   RESULTS

213   Precipitation, temperature and prey abundance

214   Neither precipitation (1989: $\overline{X}$ = 71.82 ± 18.17; 1990: $\overline{X}$ = 73.17 ± 15.50; t = -.057, P =

215   0.955) nor temperature (1989: $\overline{X}$ = 28.87 ± 0.27; 1990: $\overline{X}$ = 28.91 ± 0.24; t = 0.116, P =

216   0.909) varied between years (Fig. 1). Twelve categories of prey were recorded for 1989 and

217   13 were recorder for 1990, therefore, there were no differences between the numbers of

218   prey categories in the environment (1989: $\overline{X}$ = 6.66 ± 0.46; 1990: $\overline{X}$ = 7.33 ± 0.35; t = -

219   1.38, P = 0.268), neither between the number of individual prey between both two years

220   (1989: $\overline{X}$ = 35.4 ± 6.22; 1990: $\overline{X}$ = 43.4 ± 7.44; t = -0.824, P = 0.419; Fig. 1). For 1989

221   there was not a relationship between growth rates (both sexes and age classes) with the

222   number of prey categories (r = 0.004, P = 0.325), nor between the number of individuals

223   (insects) in the environment (r = 0.007, P = 0.228), nor with precipitation (r = 0.001, P =

224   0.557) and temperature (r = 0.011, P = 0.120). While that for 1990, there was not

225   relationship between growth rates and number of prey categories (r = 0.001, P = 0.335),

226   and number of insects in the environment (r = 0.001, P = 0.348), however, there was a

227   significant relationship between growth rates with precipitation (r = 0.012, P < 0.05), but

<div align="center">10</div>

228   not with the temperature ($r = 0.001$, $P = 0.340$). For the wet and dry seasons of 1989, 10

229   prey categories were recorded in both, and the wet season of this year had the highest

230   number of insects for each prey category. In contrast, for the wet season of 1990, 11 prey

231   categories were recorded and 12 for dry season (Table 2). Similar to the wet season of

232   1989, the wet season of 1990 had a higher number of insects for each prey category than

233   the dry season (Table 2).

234   On the other hand, there was not a significant relationship between precipitation and

235   the number of prey categories in the environment ($r = 0.026$, $P = 0.611$), or between the

236   number of individuals of each prey category ($r = -0.470$, $P = 0.885$) for 1989. There was

237   not a significant relationship between temperature and the number of prey categories in the

238   environment ($r = 0.275$, $P = 0.387$), but there was a significant relationship between

239   temperature and the number of individuals by prey category ($r = 0.533$, $P = 0.05$). There

240   was a correlation between precipitation and the number of prey categories in 1990 ($r =$

241   0.575, $P < 0.05$), but not with precipitation and the number of individuals of each prey

242   category ($r = -0.138$, $P = 0.670$). Finally, there was no correlation between temperature and

243   the number of prey category in the environment ($r = -0.167$, $P = 0.605$) or between

244   temperature and the number of individuals of each prey category ($r = -0.002$, $P = 0.993$).

245

246   Growth analysis

247   Figure 2 shows body growth rates observed and estimated for males (hatchlings, juveniles,

248   and adults; Fig. 2a) and females (Fig. 2b) for 1989 and 1990. Logistic-by-length model

249   provided the fit to the data for males, therefore that for females, the best fit to the dates of

250   growth was shows for Von Bertalanffy model (Table 3). The Von Bertalanffy model

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251   indicated that females grew slow ($r = 0.0017 \pm 0.00036$) than males ($r = 0.0053 \pm$

252   0.00040). However, these (females) reached a slightly larger size ($A_1 = 51.79 \pm 3.9422$)

253   than males ($A_1 = 46.46 \pm 0.9040$; Table 3, Fig. 2a–b).

254   Furthermore, we detected four groups of females with different growth rate, females

255   that showed a higher growth rate than other females, reaching the minimum SVL at sexual

256   maturity at an earlier age. The first group was a sample of 18 (6 %) females captured as

257   juveniles, which were recaptured several times as adults between February 1989 and June

258   1990; this group showed a growth rate of 0.083 mm/day and reached the minimum size at

259   sexual maturity (37 mm SVL) in 80 days. The second group was represented by a sample

260   of 30 females between juveniles and adults (9.3 %) recaptured between April 1989 and

261   June 1990, and showed a higher growth rate (0.16 mm/day), reaching the minimum SVL at

262   60 days after the first capture; and the third group of 89 (28 %) females classified between

263   juveniles and adults, which had a relatively high growth rate (0.70 mm/day). The rest of the

264   females (the fourth group) showed the lowest growth rate (0.0022 mm/day).

265   The logistic-by-weight model showed the best fit to analysis of the estimated

266   parameters with capture-recapture data together (hatchlings, juveniles and adults) for

267   females and males from 1989 and 1990 (Table 4). Based on this information, we observed a

268   significant overlap of confidence intervals mainly for the asymptotic growth parameter (A_1;

269   Fig. 3a), and slightly for the characteristic growth parameter (r; Fig. 3b) between both

270   sexes. Therefore, we assumed that there are differences between sexes in relation to growth

271   pattern, and therefore we developed one growth curve for each sex (Fig. 4a–b). The figure

272   4a indicate that females at a SVL of 37 mm at an age of 270 days (nine months), while that

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273   the males reached the minimum size at sexual maturity at a SVL of 35 mm at an age of 210

274   days (seven months; Fig. 4b).

275   Finally, based on the residuals obtained from models that represented the best fit of

276   growth rates for each sex and age class, and using Student´s t-test it was not possible to

277   identify differences in growth rate of hatchlings between the wet season of 1989 and the

278   dry season of 1990 (t = -0.068, P = 0.947; Table 4); however, the average size of growth

279   was greater for hatchlings during the wet season of 1989. Also, based on a two-way

280   ANOVA, differences were not found in growth of juveniles between sexes (ANOVA, $F_{1,263}$

281   = 0.087, P = 0.768), between seasons (ANOVA, $F_{1,263}$ = 2.536, P = 0.113), or years

282   (ANOVA, $F_{1,263}$ = 0.190, P = 0.663); however, the highest average values in the growth

283   rates of males and females in both years were during the wet season (Table 4). In the case

284   of adults, no differences were found in growth between sexes (ANOVA, $F_{1,414}$ = 0.001, P =

285   0.975), seasons (ANOVA, $F_{1,414}$ = 0.835, P = 0.361), or years (ANOVA, $F_{1,414}$ = 0.190, P =

286   0.989); however, the average value of adult females from 1989 and 1990 was greater in the

287   wet season (Table 4). Conversely, the highest value for average growth for males from

288   1989 was in the wet season, and for 1990 was in the dry season (Table 4).

289

290   DISCUSSION

291   The analyses on growth of hatchlings, juveniles, adults, and between years in this study

292   were based on the criterion that the best estimate of growth rate was made from those

293   models that present the lowest mean square residuals (Dunham, 1978; Schoener &

294   Schoener, 1978). Therefore, the Von Bertalanffy and logistic-by-length models equations

295   described the best growth pattern for this population. Both models provided the best fit to

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296   the data of males and females for both years (Table 2). This growth pattern is similar to that

297   observed in other lizards of the genus *Anolis* from both island and mainland environments

298   (Schoener & Schoener, 1978), who displayed an asymptotic growth when they reached

299   sexual maturity, a critical time that demands a large amount of energy invested on

300   reproduction, and which is distributed in the production of gonads but also in the

301   continuous growing process (Schoener & Schoener, 1978; Andrews, 1982; Adolph &

302   Porter, 1996). Our results for that size at sexual maturity and the maximum size reached by

303   males and females across all years were similar to those reported by Siliceo-Cantero &

304   García (2014) on males and females of *A. nebulosus*; however, the authors do not reveal

305   more detail of the growth of the different age classes for this species, neither between

306   seasons (rain-dry) nor years.

307   Roff & Fairbairn (2007) noticed that the body growth is connected with other life

308   history characteristics, such as age at sexual maturity, number and size of hatchlings,

309   parental investment, fecundity, among others; reflecting a physiological trade-off which

310   such features of fitness compete for energy (slow growth rate generate low fecundity;

311   Shine, 1989; Stearns, 1992). Therefore, in females of *A. nebulosus* as in other lizard

312   species, a slow growth rate (Warne & Charnov, 2008) could be a *trade-off* situation; for

313   example, Hernández-Salinas & Ramírez-Bautista (2015) found that females from island

314   populations were larger in SVL (from populations with slow growth, according to Tinkle,

315   1969) having larger egg mass and volume than their counterpart from mainland, but the

316   former had lower clutch frequencies, and the latter were smaller in SVL (fast growing) with

317   a higher clutch frequency and a smaller egg mass. These differences in reproductive

318   characteristics are attributed to different growth patterns, which in turn may be due to

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319   relaxation of predation and scarce interactions with other island species, while those found

320   in mainland can face higher predation intensity and interspecific competition, and therefore,

321   females from our population of study follow one of the two great predictions by Tinkle

322   (1969). For example, species of small sizes have a smaller egg mass and volume,

323   developing a pattern of fast growth which allows a fast transition from juvenile to adult

324   stage and thus avoid strong predation. This strategy has also been observed in females of

325   *Sceloporus occidentalis* (Sinervo, Hedges, Adolph, 1991).

326   Moreover, Dunham (1978) found that variation in growth rate between males and

327   females from the same species and population reflect sexual dimorphism, and usually male

328   attain larger SVL (Andrews, 1982; Zamora-Abrego, Zúñiga-Vega & Ortega-León, 2012).

329   Although males of *A. nebulosus* from this study (together data; hatchlings, juveniles and

330   adults) showed a higher growth rate, however there is no categorical evidence that this

331   growth pattern is due to sexual selection (Ramírez-Bautista & Vitt, 1997; this study). In

332   these sense, sexual dimorphism in *A. nebulosus* could be expressed in other morphological

333   characteristics, such as in color pattern of dewlap, which is more colorful (intense orange)

334   and larger in males than in females (Ramírez-Bautista, 1995).

335   Conversely, slow growth rate and late maturity of females (almost three months

336   later than males, together dates) indicates a possible continuous growth, and thus an

337   asymptotic parameter (A_1) slightly greater than males. This pattern is likely due to females

338   growing to attain the stage of vitellogenesis and receive the courtship and mating, so they

339   also continue to grow since complete development of the gonads occurs as they grow

340   (considering that this species belongs to the group with a short-life span they only survive a

341   single reproductive season; Dunham, 1978; Ramírez-Bautista, 1995; Ramírez-Bautista &

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342   Vitt, 1997). Females have an infundibulum (Ramírez-Bautista, 1995; Lozano, Ramírez-

343   Bautista, Uribe, 2014), which stores the sperm to fertilize their eggs much later (Ramírez-

344   Bautista, 1995; Ramírez-Bautista & Vitt, 1997). Thus, rapid growth of males can be

345   explained under the assumption that they need to accelerate their growth to establish and

346   defend their territory against invaders by agonistic fighting or/and for access to females for

347   mating, which demands high energy expenditure, and consequently affecting their growth

348   rate (April-May; Ramírez-Bautista, 1995; Ramírez-Bautista & Vitt, 1997).

349   On the other hand, regardless of no statistical differences found between

350   precipitation and food in the environment, the higher average values of growth rate for

351   hatchlings and juveniles of both sexes were observed in the wet season of both 1989 and

352   1990. This pattern is similar to that found by Andrews (1982) who mentioned that the

353   highest lizard growth rates are observed during the wet season because of greater food

354   availability. However, it is important to consider the quantity of fat and water (energy)

355   found in each prey category consumed by individuals of this population during the years of

356   the study, which could indicate with greater certainty a relationship of growth rate, as was

357   observed in the correlation between growth rates (sexes and age classes together) and

358   precipitation for 1990. This support the assumption that precipitation is one of the main

359   factors involved in growth rates in this species, as in other species (*A. carolinensis*,

360   Goodman, 2010; *Sceloporus grammicus*, Lemos-Espinal & Ballinger, 1995; *S. virgatus*,

361   Smith, 1995).

362   Adult females of 1989 showed a higher growth rate in the dry season, and males of

363   the same year in the wet season, but the opposite pattern occurred in females and males

364   from 1990. These data suggest that females and males could not feed steadily (in a similar

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365   way) between years as do hatchlings and juveniles, or it could also be attributed to groups

366   of adults monopolizing food among years, sites and seasons (Andrews, 1976, 1979).

367   There was no significant correlation between environmental variables (precipitation

368   and temperature) and the amount of food available in the environment. Nonetheless, we

369   believe that these variables directly or indirectly influence the growth of *A. nebulosus* of

370   this sampled population, as it occurs in *A. oculatus* and *A. limifrons* from island and

371   mainland habitats, where differences in growth rate of these species were identified

372   (Andrews, 1976). These results were attributed to differences in availability and selection

373   of food, noting that food was more plentiful on mainland than on the island, and therefore

374   juveniles of *A. limifrons* from mainland grew at a faster rate than *A. oculatus* from the

375   island (Andrews, 1976). Thus, both situations could be taking place in the juveniles of *A.*

376   *nebulosus* from this study. Additionally, groups of adult females with higher growth rates

377   reflect that they arrived before than other individuals and settled on the sites (trees) that

378   showed the best conditions for feeding and breeding (Ramírez-Bautista, 1995; Ramírez-

379   Bautista & Vitt, 1997; Ramírez-Bautista & Benabib, 2001).

380   Although we do not present sufficient data on reproduction, one reason that might

381   explain variations in growth rate between males and females of *A. nebulosus* is the

382   minimum SVL at sexual maturity, which is attained faster in males than females as an

383   important strategy to increase their reproductive success by mating with the biggest number

384   of females as possible during the single breeding season, and consequently increasing their

385   fitness (Ramírez-Bautista, 1995; Ramírez-Bautista & Vitt, 1997). Another reason could be

386   related to environmental pressures, the anole species inhabiting islands have a slower

387   growth rate than mainland ones (Andrews, 1976, 1979), this is a feature that occurs when

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388   food is more scarce on the islands than on mainland (Schoener & Schoener, 1978;

389   Andrews, 1982). Furthermore, the intensity of predation usually is stronger on the continent

390   than in islands, and for this reason lizards in continental environments should grow faster to

391   reach sexual maturity at smaller sizes as a strategy to reduce likelihood of predation

392   (Zúñiga-Vega et al., 2007). Therefore, the availability of food and predation intensity in the

393   environment, are two factors that play an important role in the variation of growth rate

394   patterns of males and females of this analyzed population.

395   Lastly, phylogeny can also regulate the beginning and end of growth for each

396   species, and although little is known about it, these anoles are able to exhibit a camouflage

397   to increase predator avoidance, have low growth rates, and individuals are agile to escape

398   from predators such as whiptail and varanid lizards (Andrews, 1982). Future studies should

399   be directed on growth rates in order to establish possible patterns among both, species and

400   populations of a single species. This will allow identifying more accurately the factors

401   influencing growth rate of lizards from tropical environments.

402

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Figure 1

Climate data (lines; precipitation in mm and temperature in °C) and food data (bars) for the study site during 1989 and 1990 from Chamela, Jalisco, Mexico.
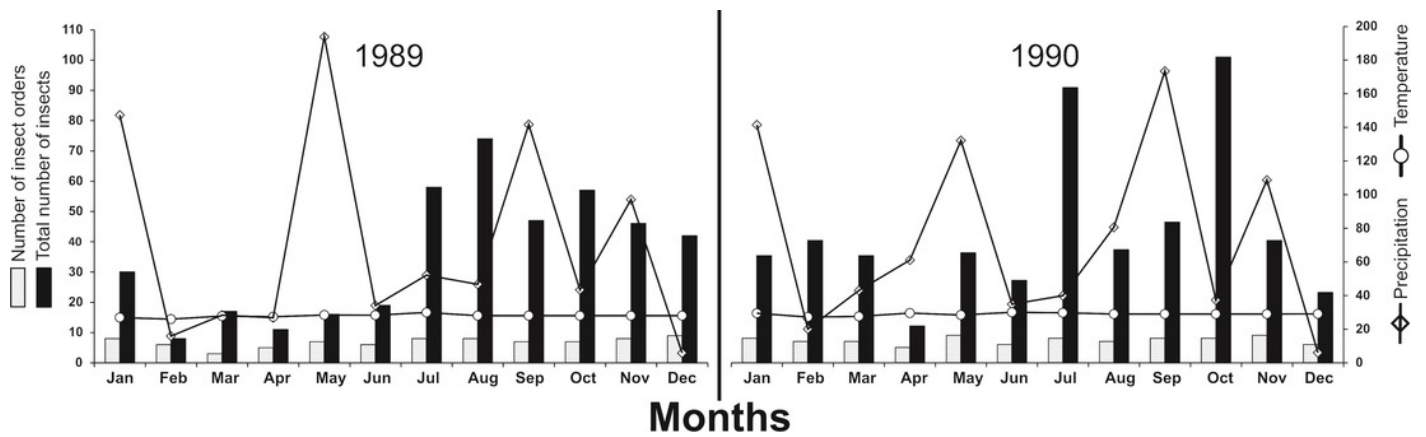
Figure 2

Comparing the estimated growth rates as a function of body length for hatchlings, juveniles and adult males together.
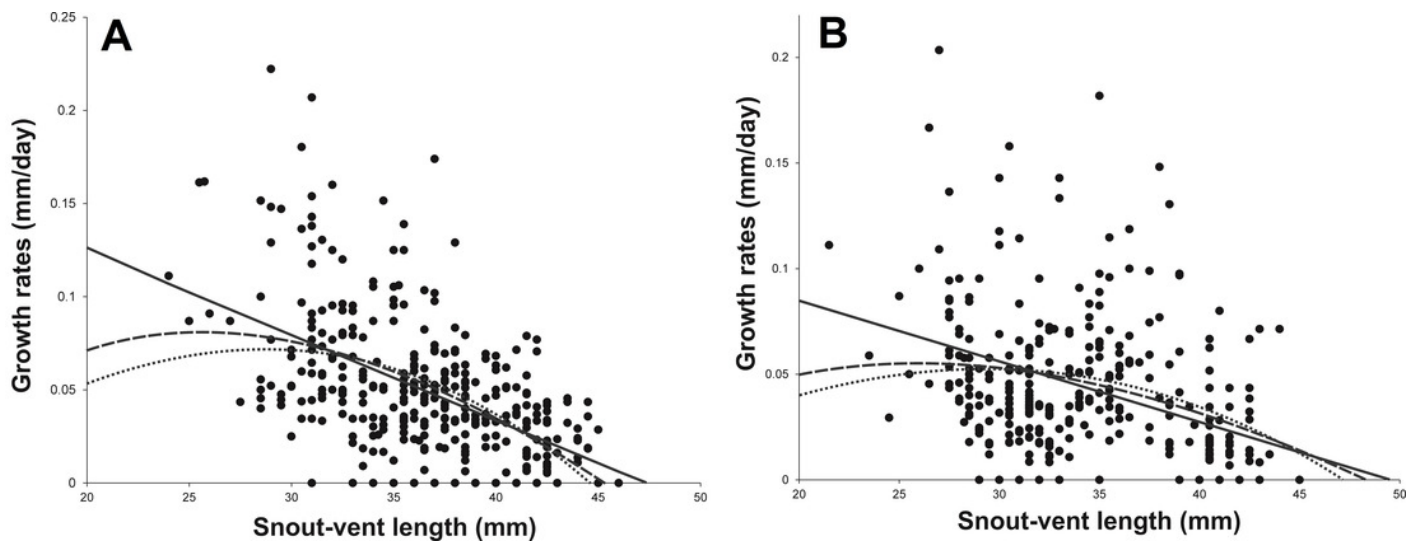
Figure 3

Comparison of asymptotic length (a) and characteristics growth parameter (b) for females and males (combined data; see text) of *Anolis nebulosus* from Chamela, Jalisco, Mexico, with 95% intervals.
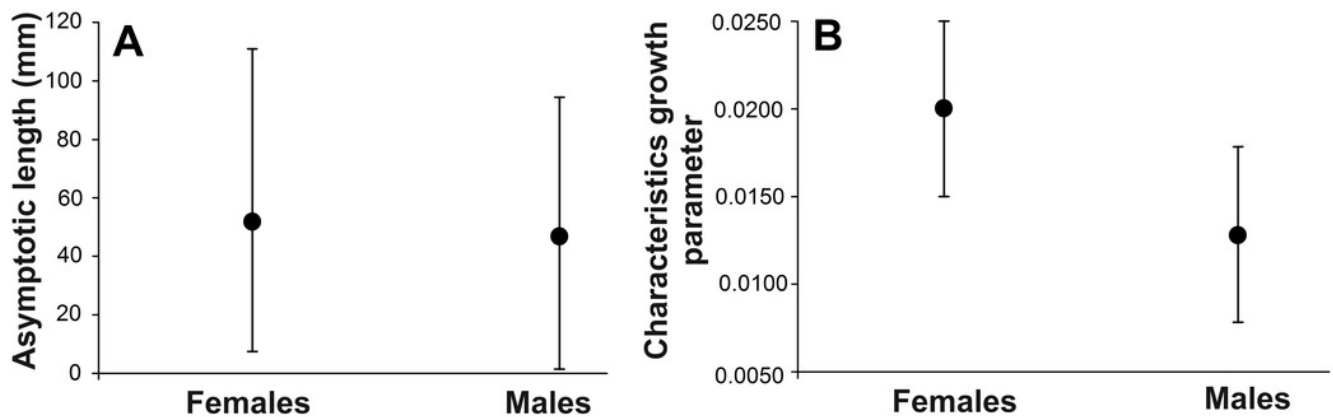
Figure 4

Growth curve estimated with logistic-by-weight model. Lines indicate the size and age at which females (a) and males (b) (combined data; see text) reach at sexual maturity in *Anolis nebulosus* from Chamela, Jalisco, Mexico.
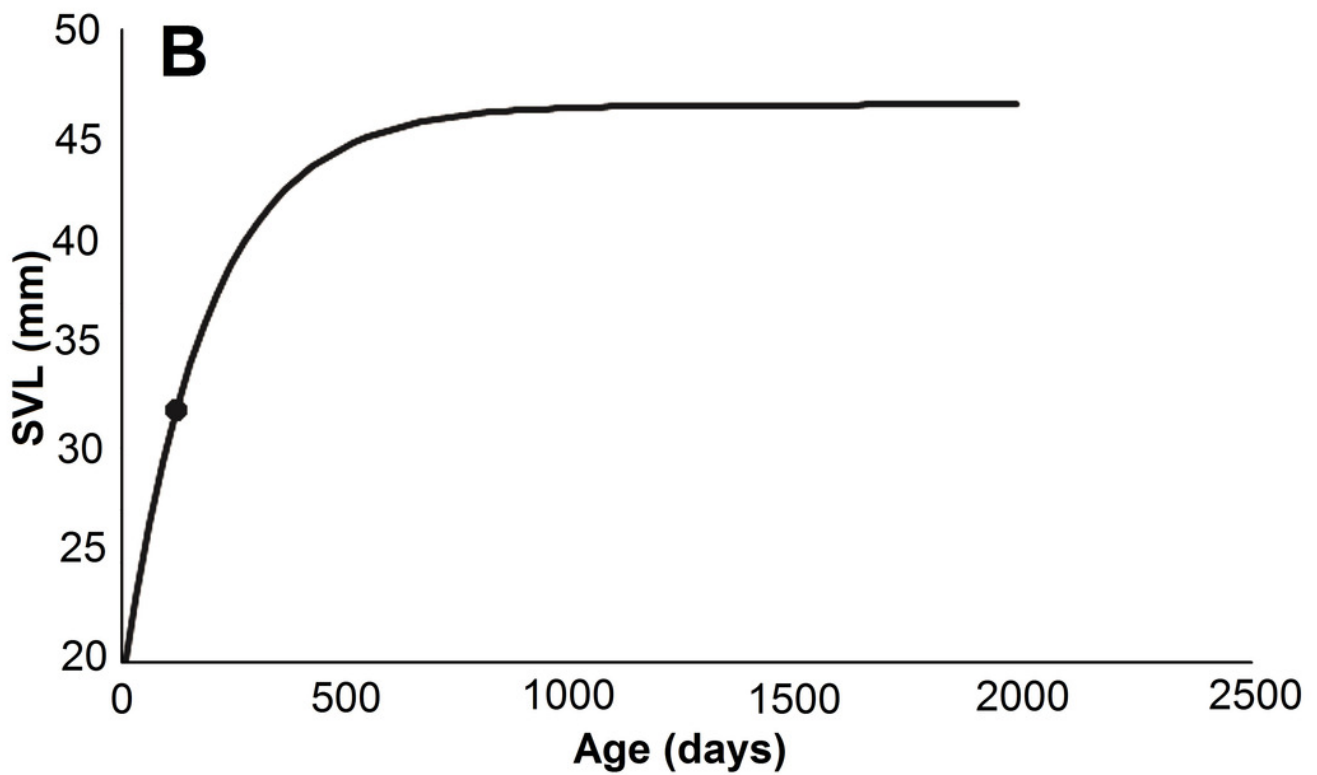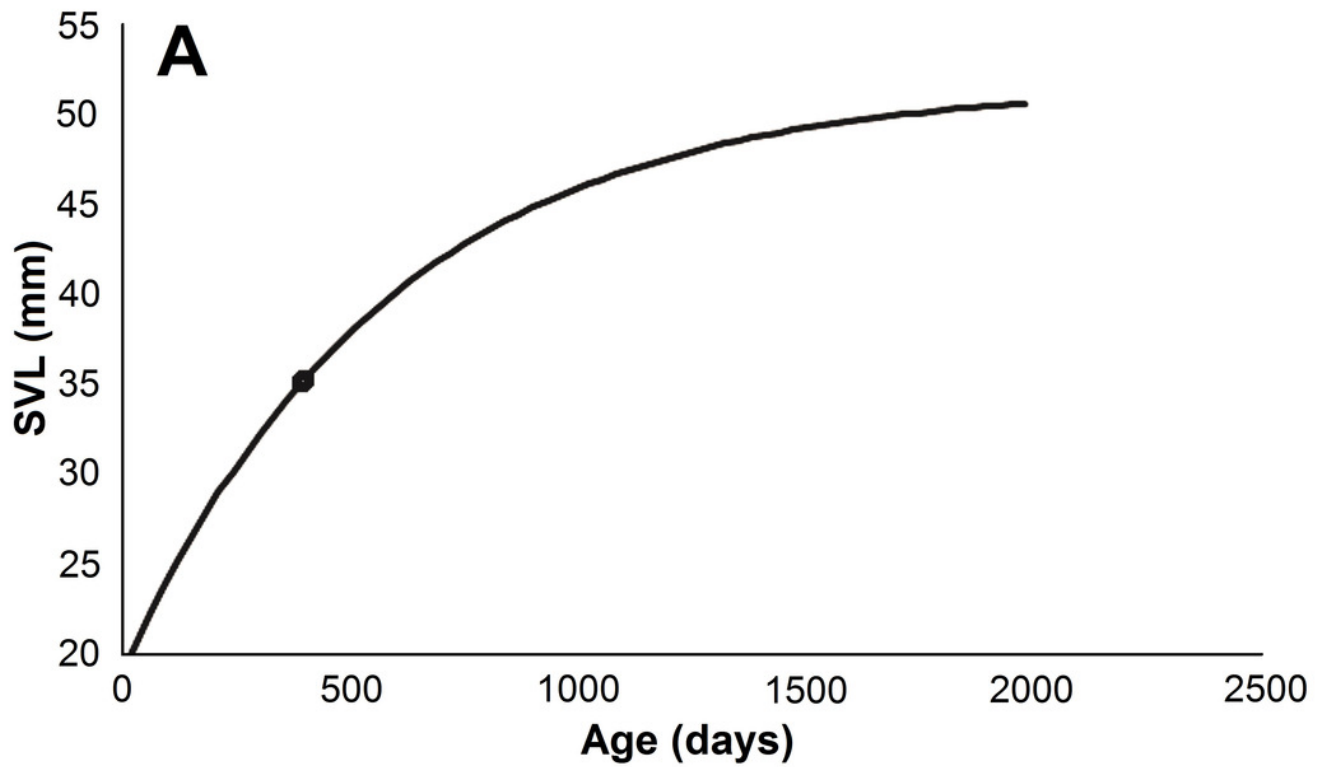
Table 1(on next page)

Mathematical description of the models evaluated in this paper

1   **Table 1 Mathematical description of the models evaluated in this paper.** GR = growth rate, L

2   = body lengths which respond to growth rate, A_1 = snout-vent length asymptotic, r = growth

3   characteristic parameter, L_0 = birth length.

	Models		
	Von Bertalanffy	Logistic-by-Length	Logistic-by-Weigth
Diferential equation	$GR = A_1r\,[1-(L/A1)]$	$GR = Lr\,[1-(L/A_1)]$	$GR = (rL/3)\,[1-(L^3/A_1^3)]$
Solution	$L = A_1\,(1-be^{-rt})$	$L = A_1\,/\,(1+be^{-rt})$	$L = [A_1^3/(1+be^{-rt})]^{1/3}$
Where	$b = (1-L_0/A_1)$	$b = (A_1/L_0)-1$	$b = (A_1^3/L_0^3)-1$

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5   Notes. The details of each model can be reviewed in Dunham (1978) and Schoener and Schoener

6   (1978).

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Table 2(on next page)

Prey categories in the environment

1 **Table 2 Prey categories in the environment**. The number of prey categories were collected
2 during the sampling years 1989 and 1990 in the region of Chamela, Jalisco, Mexico.

	Food resource in the environment					
Prey category	1989	Wet Season	Dry Season	1990	Wet Season	Dry Season
Acaridae	1		1			
Aranae	161	121	40	167	88	79
Coleoptera (A)	57	49	8	40	29	11
Coleoptera (L)	7	6	1	4	3	1
Diptera	34	31	3	37	29	8
Dermaptera				1		1
Hemiptera	30	25	5	32	25	7
Homoptera	20	14	6	80	66	14
Hymenoptera	53	40	13	61	54	7
Isoptera	1	1				
Lepidoptera (A)	2		2	19	19	
Lepidoptera (L)	11	11		10	8	2
Orthoptera	48	43	5	56	33	23
Psocoptera				1		1
Thysanoptera				3	2	1
Total	425	341	84	511	356	155

3 Notes. Numbers represent abundance of individuals collected for each prey category. Adult = A,
4 Larvae = L.
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Table 3(on next page)

Summary of growth parameters

1   **Table 3 Summary of growth parameters for each model in the analysis of growth for *Anolis***

2   ***nebulosus* from Chamela, Jalisco, Mexico**.

	Model	MSR	R^2	A_1	r
Males (351)	Von Bertalanffy	0.3144	0.1464	50.36 ± 1.8599	0.0028 ± 0.00037
	Logistic by length	0.3116	0.1538	46.46 ± 0.9040	0.0053 ± 0.00040
	Logistic by weight	0.3122	0.1522	45.07 ± 0.6141	0.0076 ± 0.00045
Females (357)	Von Bertalanffy	0.3755	0.0619	51.79 ± 3.9422	0.0017 ± 0.00036
	Logistic by length	0.3813	0.0467	47.35 ± 1.9404	0.0033 ± 0.00036
	Logistic by weight	0.3855	0.0364	45.49 ± 1.2822	0.0051 ± 0.00041

3   Notes. MSR = residuals error mean square, R^2 = determination coefficient, A_1 = asymptotic

4   growth parameter, r = growth characteristic parameter.

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Table 4(on next page)

Seasonal and annual variation in growth rates

1 **Table 4 Seasonal (Dry and Wet) and annual variation in growth rates of *A. nebulosus*.** F =

2 females, M = males.

Age class / Sex	1989		1990	
	Dry	Wet	Dry	Wet
Hatchlings				
F and M	-----	-0.0023 ± 0.084	-0.00025 ± 0.047	-----
Juveniles				
F	-0.004 ± 0.003	-0.013 ± 0.011	0.000047 ± 0.030	-0.001 ± 0.003
M	-0.008 ± 0.023	-0.012 ± 0.017	-0.000086 ± 0.020	-----
Adult				
F	-0.009 ± 0.005	0.004 ± 0.007	-0.008 ± 0.004	0.005 ± 0.005
M	-0.001 ± 0.003	0.003 ± 0.007	0.003 ± 0.002	-0.009 ± 0.003

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