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Reproduction in the Green Anole, *Anolis carolinensis* (Squamata: Dactyloidae), from Hawaii

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Abstract: Reproduction was studied in an invasive population of *Anolis carolinensis* in the Hawaiian Islands, USA. Timing of events in the reproductive cycle was similar between *A. carolinensis* populations in Hawaii and native populations of the species in the southeastern United States. In Hawaii, males of *A. carolinensis* undergo a prolonged period of spermiogenesis (sperm formation) starting in November (n=1) and December (n=1) and continuing into August. Gravid *A. carolinensis* females in Hawaii (n=40) produce one egg in continuous succession from March into August. Reproductive activity in *A. carolinensis* in Hawaii ceased prior to the colder, wetter, winter months.

Key words: *Anolis carolinensis*; Egg production; North America; Reproductive Cycle; Seasonal spermatogenesis

Introduction

Anolis carolinensis is native to the southeastern United States and has been introduced to and established in Pacific Islands (Northern Marianas, Federated States of Micronesia, Guam, Hawaii, Ogasawara, Palau, and Okinawa), and West Indies (Grand Bahama Island, Anguilla) (Kraus, 2009). Shaw and Breese (1951) reported *A. carolinensis* in Oahu, Hawaii in 1951. Within Hawaii, it is now found on Oahu, Lanai, Maui, Hawaii Island, Kauai, and Molokai (McKeown, 1996; Kraus, 2002).

Despite its successful colonization in the Hawaiian Islands, its effects on local plants and animals are unknown, but can be significant elsewhere. For example, in the Ogasawara Islands (ca. 1000 km S of Tokyo, Japan), it has caused serious destruction of the endemic insect community through predation (Toda et al., 2013). Therefore, it is necessary to understand the reproductive ecology of *A. carolinensis* in the Hawaiian Islands before a management plan can be formulated to manage this invasive species. In this paper we present data on reproduction of *A. carolinensis* from Hawaii utilizing a histological examination of gonadal material. Comparisons are made with the timing of the *A. carolinensis* reproductive cycles in the southeastern United States versus Hawaii.

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Materials and Methods

We examined a sample of 175 *A. carolinensis* consisting of 91 adult males (mean snout-vent length [mean SVL]=66.0 mm±4.4 SD, range =51–76 mm), 58 adult females, (mean SVL= 52.5 mm±3.8 SD, range=47–73 mm), 10 female subadults with no reproductive activity (mean SVL=40.9 mm±2.5 SD, range=38–44 mm) and 16 unsexed juveniles (mean SVL=29.9 mm±6.1 SD, range=21–40 mm) collected from 1961 to 2010 from Hawaii, USA, and deposited in the herpetology collections of the Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii, USA, Natural History Museum of Los Angeles County (LACM), Los Angeles, California, USA, and University of Michigan, Museum of Zoology (UMMZ), Ann Arbor, Michigan, USA. Within Hawaii the specimens were collected from the following islands: Hawaii (n=15), Kauai (n=19), Maui (n=31), Molokai (n=12), and Oahu (n=98).

A slit was made in the left side of the abdomen and the left testis was removed from males and the left ovary was removed from females for histological examination. Enlarged vitellogenic pre-ovulatory ovarian follicles (>3 mm) or oviductal eggs were counted in situ. No histology was performed

Table 1. Monthly stages in the testicular cycle of 91 adult male *Anolis carolinensis* from Hawaii, USA.

Month	N	Regression	Recrudescence	Spermiogenesis
January	7	1	0	6
February	5	0	0	5
March	22	0	0	22
April	8	0	0	8
May	2	0	0	2
June	20	0	0	20
July	18	0	0	18
August	6	4	0	2
October	1	0	1	0
November	1	0	0	1
December	1	0	0	1

Table 2. Monthly conditions in the gonads of 40 reproductively active adult females of *Anolis carolinensis* from Hawaii, USA.

Month	N	One oviductal egg	Two oviductal eggs	Oviductal egg and follicle >3 mm	One enlarged follicle >3 mm	Two enlarged follicles >3 mm
March	5	1	0	2	1	1
April	5	0	2	2	1	0
May	4	0	0	4	0	0
June	16	5	7	4	0	0
July	5	2	1	2	0	0
August	3	0	1	1	1	0
September	1	0	0	0	1	0
October	1	1	0	0	0	0

on them. These enlarged (>3 mm) follicles were opened with a razor blade and were filled with yolk. There is a high probability that follicles of this size would have grown larger through accumulation of additional yolk and ovulated (Goldberg, 1973). Removed gonads were embedded in paraffin, cut at 5 µm, and stained by Harris' hematoxylin followed by eosin counterstain (Presnell and Schreibman, 1997). Descriptive terminology for stages in the testicular and ovarian cycles (Tables 1 and 2) is SRG's original and was utilized in numerous previous publications (Goldberg, 2013; Goldberg and Grismer, 2015; Goldberg and Kraus, 2016). Slides of the testes were categorized according to the stage of the testicular cycle (Table 1) (Goldberg, 2005). Epididymides of examined testes were not available for histological examination. Slides of ovaries were examined for yolk deposition and categorized as to the stage of the ovarian cycle (quiescent or early yolk deposition) (Goldberg, 2005). We separated reproductively active females into five stages (Table 2). Histology slides were deposited in the herpetology collections of the Bernice B. Bishop Museum (BPBM), Natural History Museum of Los Angeles County (LACM), and University of Michigan, Museum of Zoology (UMMZ).

Results

Three stages were present in the *A. carolinensis* testis cycle (Table 1): (1) Regression, in which germinal epithelium within the seminiferous tubules is reduced to a few layers of spermatogonia and interspersed Sertoli cells; (2) Recrudescence, in which a proliferation of germ cells for the next period of spermiogenesis has commenced. In early recrudescence, primary spermatocytes are dominant; in late recrudescence secondary spermatocytes and spermatids predominate; (3) Spermiogenesis, in which the lumina of the seminiferous tubules are lined by sperm or clusters of metamorphosing spermatids. Males undergoing spermiogenesis were found in all months except October (n=1) although sample sizes were smaller in autumn and winter (Table 1) when low temperatures in Hawaii limited activity. All adult males in Hawaii (75/75) were reproductively active (exhibited spermiogenesis) from February through July. The testicular cycle ended in August when 67% (4/6) males exhibited regressed testes. While we did not histologically examine epididymides, all of these structures were enlarged in reproductively active males whereas they were reduced in size in the five males with regressed testes (Table 1). Both of the two smallest reproductively active males (exhibiting spermiogenesis) measured 53 mm SVL and were collected in June (BPBM 14782) from Kauai and March (UMMZ 224427) from Maui.

Five stages were utilized to describe the gonadal conditions in reproductively active females (Table 2): (1) With one oviductal egg and no enlarged (>3 mm) ovarian follicles; (2) Two oviductal eggs and no enlarged (>3 mm) ovarian follicles; (3) One oviductal egg and one enlarged (>3 mm) ovarian follicle; (4) No oviductal eggs and one enlarged (>3 mm) ovarian follicle; (5) No oviductal eggs and two enlarged (>3 mm) ovarian follicles. Oviductal eggs and concurrent enlarged (>3 mm) follicles were observed in 38% (15/40) of reproductively active females (Table 2), indicating *A. carolinensis* produces eggs in succession in Hawaii. In cases of two oviductal eggs in the same female (28% [11/40]) they were never in the same stage of development, i.e., one egg was shelled and close to being deposited, whereas the other egg was unshelled. Also, there was alternate use of oviducts, i.e., in no cases were two oviductal eggs found in the same oviduct. Reproductively active females were found from March to October (Table 2). The months of maximum female reproductive activity in Hawaii was May–July when all 4, 16, and 5 females contained oviductal eggs, respectively (Table 2). Two other stages were noted in the ovarian cycle in non-reproducing females: (1) Quiescent or no yolk deposition, January (n=1) and December (n=1); (2) Early yolk deposition, basophilic yolk granules in the ooplasm, March (n=1) and October (n=1). The smallest reproductively active female measured 48 mm SVL (UMMZ 226757), contained oviductal egg and one enlarged follicle (>3 mm), and was collected in July on Oahu.

Discussion

In Hawaii, *A. carolinensis* males exhibit a prolonged period of sperm formation that runs from January into August, thereby allowing for repeated insemination of females. In Hawaii, *A. carolinensis* reproduction ceases during the cool, wet winter when few animals are active. This is comparable to what occurs in its native range in the southeastern United States (Powell et al., 2016). Early works on *A. carolinensis* reproduction in the latter region (Hamlett, 1952; Dessauer, 1955; Fox, 1958) utilized specimens from New Orleans, Louisiana. Hamlett (1952) described a prolonged breeding season (mid-spring until the end of summer) with production of single eggs in regular succession. Production of single eggs occurs also in other *Anolis* species (Smith et al., 1972). Fitch (1982) believed that carrying only one mature egg at a time put a minimum burden on *Anolis* females and did not hinder their climbing ability.

For a native population of *A. carolinensis*, Dessauer (1955) recorded minimal testes and ovarian weights from September–October, and from September–February, respectively. These were months when few *A. carolinensis* were active (Dessauer, 1955). Fox (1958) reported maximum testes sizes occurred in spring followed by decreases in June through August; minimum sizes were in September to October followed by size increases in late autumn (November) and winter (February). Timing of events in the *A. carolinensis* testis cycle are typical of those seen in other temperate zone lizards in which gonads regress in late summer, followed by renewal (recrudescence) in fall and spermiogenesis in spring (Goldberg, 1974). As we have no histological data on amounts of sperm in epididymides from *A. carolinensis* with regressed testes, we cannot evaluate whether additional mating occurs utilizing stored epididymal sperm (*sensu* Méndez de la Cruz et al., 2015). Factors responsible for regulation of the testis cycle in *A. carolinensis* in the southeastern United States are supposedly decreasing day lengths in late summer resulting in testis regression (Licht, 1971) and the temperature increase in early spring that stimulates testicular activity (Crews, 1980). Females emerge several weeks later and establish home ranges (Gordon, 1956).

It is thus known that *A. carolinensis* has a seasonal reproductive cycle in the southeastern United States with reproduction in spring to mid-summer (May–July) and non-breeding in the remaining season of the year (Jenssen et al., 1995). Reportedly, *A. carolinensis* females can produce one egg every two weeks during the breeding season in Georgia, U.S.A. (Jensen et al., 2008).

From the preceding, it appears that the timing of the reproductive cycle of *A. carolinensis* in Hawaii is similar to that of conspecifics in the native region with continuous reproduction in spring through summer and reduced levels beginning in late summer and continuing through fall (Dessauer, 1955). In Hawaii, the timing of the *A. carolinensis* reproductive cycle is in synchrony with the local climate which consists of two seasons, summer (the warm season) including May through September and winter (the cool season) from October through April, characterized by cooler temperatures and extensive rains (Juvik and Juvik, 1998).

A period of reduced autumn reproductive activity was also exhibited by introduced populations of the brown anole, *Anolis sagrei* in Hawaii (Goldberg et al., 2002), and the common house gecko, *Hemidactylus frenatus* (Goldberg and Kraus, 2016) during fall–winter, suggesting a shared response to changing environmental conditions. Reproductive cycles in Hawaiian populations of *A. carolinensis* and the congener *A. sagrei* show similar seasonality to that seen in native populations (Fox, 1958; Sexton and Brown, 1977), whereas the seasonality seen in *H. frenatus* contrasts with the continuous breeding shown in its native tropical range where reproduction occurs throughout the year (Hamlett, 1952; Church, 1962; Gaulke, 2011).

In conclusion, the reproductive cycle of nonnative *A. carolinensis* in Hawaii follows the pattern described for this species in the native range of the southeastern United States, as both males and females of the species exhibit a prolonged period of reproduction as reported in other *Anolis* species (Licht and Gorman, 1970). Females of *A. carolinensis* in Hawaii produce single eggs in succession as seen in other species of *Anolis* (Smith et al., 1972).

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Appendix

Museum accession numbers for the specimens of *Anolis carolinensis* from Hawaii examined by island from the Bishop Museum (BPBM), Honolulu, Hawaii, USA, the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, USA, and the University of Michigan, Museum of Zoology (UMMZ), Ann Arbor, Michigan, USA. Hawaii Island: BPBM 6533, 10598–10961, 11084, 11085, 23966, 28100; LACM 145404–145407; UMMZ 226918, 226919; Kauai: BPBM 11472, 11473, 11537, 13086–13088, 14780–14792; UMMZ 227380. Maui: BPBM 12203–12206, 13721, 13722, 13843, 13844 13980, 13982, 13984, 27314–27318, 35338, 35339, 35658; UMMZ 224424–224427, 225263, 225265, 225266, 225269, 226764, 226767, 226768, 227378. Molokai: BPBM 23930–23933, 23952, 28101–28107; Oahu: BPBM 689, 1934, 4996, 8314, 8380, 8569, 11168, 14362, 21133, 21134, 23598, 31557–31589, LACM 145390, 145391, 145393, 145394; UMMZ 224427–224429, 225261, 225264, 225267, 225268, 226739, 226740, 226742–226763, 226765, 226766, 226769–226771, 226772–226774, 227377, 227379, 227381–227387, 227420.

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