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Observations on Nesting and Clutch Size in *Furcifer oustaleti* (Oustalet's Chameleon) in South Florida

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Abstract - We studied an established population of *Furcifer oustaleti* (Oustalet's Chameleon) in southeastern Florida to understand aspects of reproductive biology in this nonnative species. Reproduction of Oustalet's Chameleon had not been documented in the field in Florida, and limited information is available about its reproduction in its native range. We conducted surveys from July 2011 to October 2012 in the *Persea americana* (Avocado) grove where this species was introduced in Miami-Dade County, FL. During these surveys, we removed more than 430 chameleons. We encountered 23 gravid females from June to October. Mean clutch size was 42.3 eggs, and we recorded a new maximum clutch size of 72 eggs. Utilizing radio-telemetry, we were able to track a gravid female to a nest cavity, and herein describe the first Oustalet's Chameleon nest in Florida. Our findings suggest that management for eradication of the species should include ongoing surveys, with removal efforts intensified from June to October, when females are known to be gravid.

Introduction

Florida has 56 established species of nonnative herpetofauna, more than any other state in the US (Engeman et al. 2011, Krysko et al. 2011). Little is known about the life history of many of these tropical and subtropical species within their native ranges. However, much less is known about how they interact with the environment in their introduced range. Significant resources are rarely spent learning about introduced species until they become invasive and cause economic, ecological, or human health or safety concerns; by then, eradication is usually expensive and nearly impossible (Byers et al. 2002, Mehta et al. 2007, Pimentel et al. 2005). Better understanding of the ecology of these species may improve the ability to develop management actions to address potential impacts.

The number of introduced species of reptiles and amphibians in the state of Florida continues to increase. Most introductions occur through anthropogenic means such as cargo transport or the pet trade (Krysko et al. 2011,Wilson and Porras 1983). Of the 56 species of established nonnative herpetofauna documented in Florida, 46 are lizards (Krysko et al. 2011), 2 of which are species of Chamaeleonidae:

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Chamaeleo calyptratus Duméril & Bibron (Veiled Chameleon; see Krysko et al. 2004) and *Furcifer oustaleti* (Mocquard) (Oustalet's Chameleon; see Gillette et al. 2010). Other chameleon species have been introduced in Florida (e.g., Engeman et al. 2005, Krysko et al. 2011, Rochford et al. 2013), but these are regarded as either extirpated or representative of isolated escapees/releases that have not formed established populations.

Oustalet's Chameleon is the second largest extant species of chameleons, reaching up to 68.5 cm total length (Glaw and Vences 1996, 2007; Nečas 2004). Although the diet of most chameleons consists primarily of arthropods (Hofer et al. 2003, Kraus et al. 2011), Oustalet's Chameleon is known to eat small vertebrates including birds (García and Vences 2002). Endemic to Madagascar, Oustalet's Chameleon naturally inhabits dry deciduous forests, wet montane savannahs, and primary forest (Glaw and Vences 2007). It also thrives in agricultural lands and anthropogenically altered landscapes (D'Cruze and Kumar 2011, Glaw and Vences 2007). This species was previously introduced into Kenya, where its current status is unknown (Nečas 2004; Spawls et al. 2002, 2014; Tilbury 2010). At least 16 y ago, Oustalet's Chameleon was introduced to a single 48-ha *Persea americana* Mill. (Avocado) grove in southwestern Miami-Dade County, FL. All size classes including neonates have been observed at this site (Gillette et al. 2010; D. Smith et al., unpubl. data).

Although the introduction of Oustalet's Chameleon in southeastern Florida has been described (Gillette et al. 2010, Krysko et al. 2011), there has been no documentation of reproduction in this population. A better understanding of the ecology and life history of the Oustalet's Chameleon may be critical for developing effective management strategies for this nonnative species. Here, we report on chronology of gravid females, nest-site characteristics, clutch size, egg characteristics, and incubation period for individuals collected in southeastern Florida.

Materials and Methods

Surveys

Our study site was a privately owned 48-ha Avocado grove located in Florida City, FL (25.433ºN 80.501ºW). Three sections of the grove were divided into 400 m x 400 m plots. Although the grove was predominantly composed of Avocado trees, we also found chameleons on *Schinus terebinthifolius* Raddi (Brazilian Pepper), *Neyraudia reynaudiana* (Kunth) Keng ex A.S. Hitchc. (Burma Reed), *Parthenocissus quinquefolia* (L.) Planch. (Virginia Creeper), *Parthenium hysterophorus* L. (Santa Maria Feverfew), and other nonnative and native plant species. The grove is bordered by a row of *Roystonea regia* (Kunth) O.F. Cook (Royal Palm) and a road to the south, an Avocado grove to the west, and roads on the northern and eastern boundaries. The Navy Wells Pineland Preserve, a natural area consisting primarily of pine-rockland habitat managed by the Miami-Dade County Parks, Recreation, and Open Spaces Department, is adjacent to the northern perimeter road (Fig. 1).

We conducted nighttime visual surveys (n = 27) with flashlights from 12 July 2011 to 15 October 2012 to remove Oustalet's Chameleons and determine their reproductive characteristics; additional data was collected for related studies. We performed surveys throughout the grove and in a section of Navy Wells Pineland Preserve to the north. Surveys began after sunset and lasted 3–4 h, depending on the number of individuals surveying and whether the survey was constrained or unconstrained. We conducted 9 unconstrained surveys throughout the study site from July to October 2011. Following these surveys, we conducted 19 distance-constrained surveys along standard routes from 20 October 2011 to 15 October 2012. Each distance-constrained survey consisted of walking 1 of 4 selected areas (1 in each of 3 plots in the Avocado grove, and 1 plot included a portion of the Navy Wells preserve) of ~12,000 m^2, 1–2 times each month. Although we did not conduct formal surveys in adjacent areas, informal visual-encounter surveys were conducted in July 2011 in all adjacent, potential sites.

When Oustalet's Chameleons were encountered, we recorded the location (GPS coordinates), size, sex, and reproductive status of females. We captured and removed all specimens unless they were too high in the trees to safely capture. We determined gravidity of females based on body size and coloration at the time of collection (see Cuadrado 2000). Gravid females have a distended abdomen and are green with colors that are not observed throughout the rest of the year, including

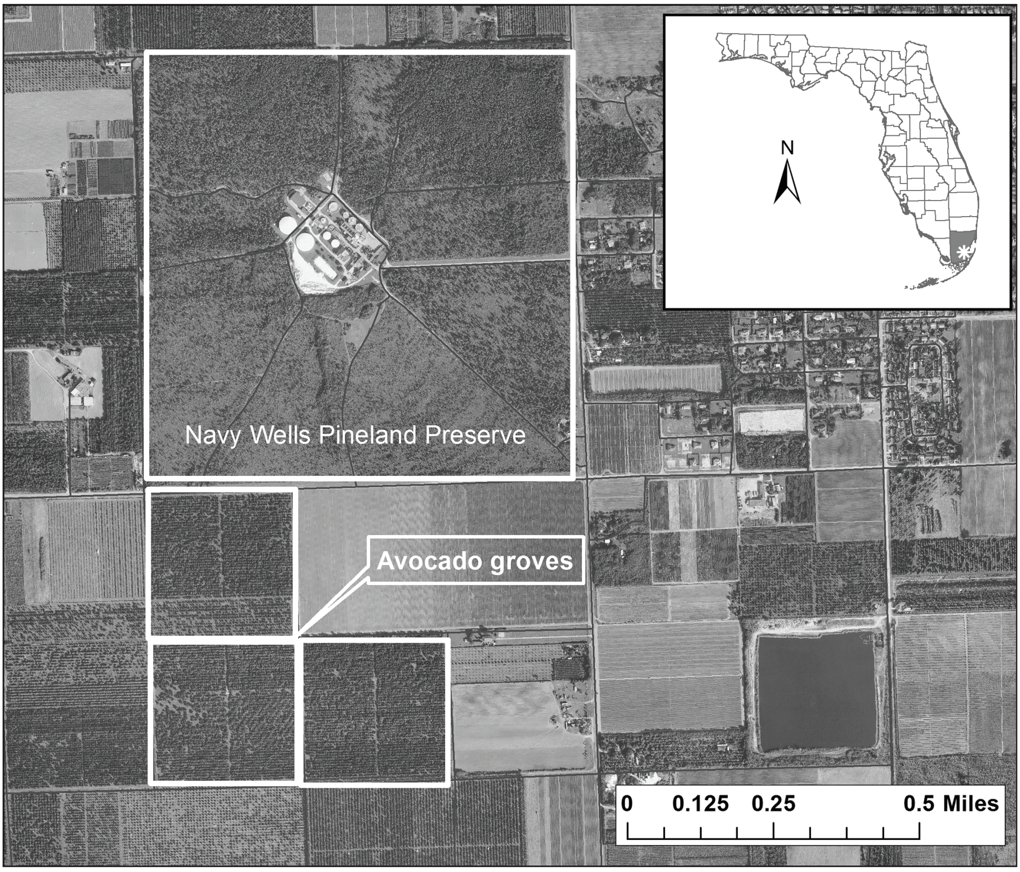

Figure. 1. Map showing three 400 m x 400 m Avocado grove plots and the adjacent Navy Wells Pineland Preserve. We established 1 survey route in each of these 4 areas.

white, red, or orange patterns (Fig. 2a). Non-gravid females have a more-slender abdomen and are green with a less colorful background pattern (Fig. 2b).

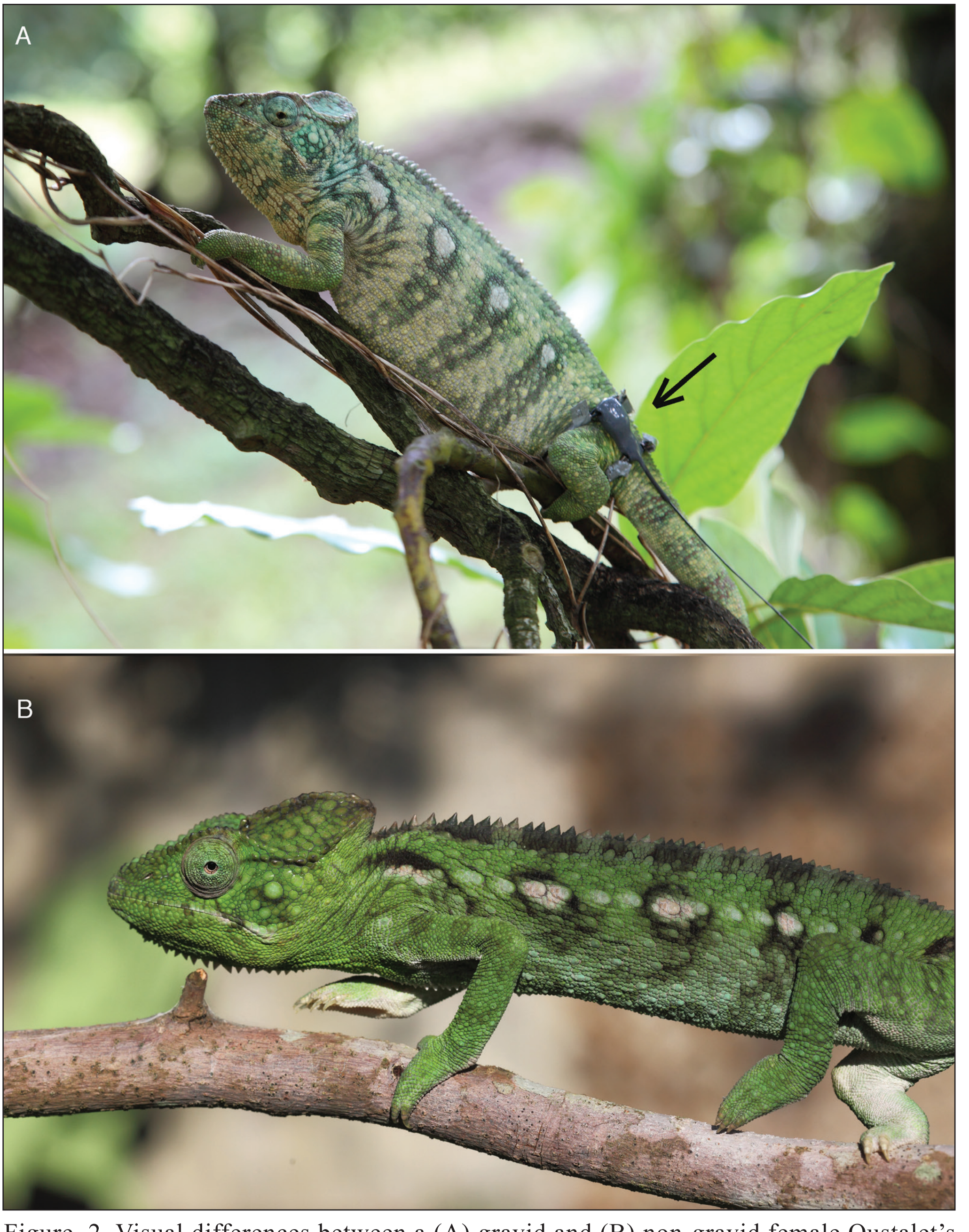

Figure. 2. Visual differences between a (A) gravid and (B) non-gravid female Oustalet's Chameleon in *Persea americana* (Avocado) trees. Note the distended abdomen and different coloration in the gravid female compared to the non-gravid female. The transmitter attachment saddle using leader line is also shown in panel A, including location and connections (arrow).

Clutch data and incubation

Gravid females were kept individually in approximately 60 cm x 60 cm x 90 cm-tall nylon-mesh-sided enclosures with live plants, full spectrum and basking lighting on a 12-h light cycle, and daily misting. We provided nesting buckets with 25–40 cm of a sand and soil mixture as oviposition sites. Following oviposition, we weighed and measured (length x width) a subsample of the eggs (n = 149) from 15 clutches. We used this subset of clutch data because females were distributed among different facilities and incomplete data were collected at some locations. Clutches from 3 females, as well as a clutch from 1 other female collected from the same site prior to the start of our surveys, were artificially incubated in deli-cup containers filled midway with a 1:1 water:vermiculite mixture by weight. No additional moisture was added to the media during the incubation period. We placed the containers inside a dark closet and allowed the eggs to incubate at ambient laboratory temperature (19–23 ºC average daily temperature range) to test the resilience of eggs to a broad range of incubation temperatures. We used linear regression analysis ($\alpha = 0.05$) and the 2-tailed Pearson product-moment correlation coefficient to test for correlations between female mass and clutch mass and between snout–vent length (SVL) and clutch size. Statistical analyses were performed in R, and means are reported as ± standard deviation (SD).

Radio-telemetry

We captured a single gravid female on 15 October 2012, affixed a VHF radio transmitter (BD-2, Holohil, ON, Canada) on its dorsal ridge, and radio-tracked her to determine oviposition location (Fig. 2a). The transmitter was attached to a saddle, created using a 2.5-mm-vinyl plastic-coated leader line. We secured the transmitter saddle over the pelvic region, with the line wrapped both cranial and caudal to her hind limbs; leader-line ends were attached to one another using a stainless steel barrel-crimp with its edges wrapped in tape (Fig. 2a). We released the specimen at the collection site on 16 October 2012 at ~1610 h. Thereafter, we tracked it daily using a handheld receiver (R-1000, Communications Specialists, Inc., Orange, CA) and Yagi antenna. We used a handheld weather meter (Kestrel Meter 3000, Nielsen-Kellerman, Boothwyn, PA) to measure the nest temperature and humidity.

Results

Chronology of reproduction

We collected 431 Oustalet's Chameleons (78 males, 81 females, and 272 unsexable juveniles) during surveys from July 2011 to October 2012. We captured a total of 23 gravid females during June (n = 6; 100% of females captured), July (n = 6; 75%), August (n = 6; 75%), September (n = 3; 21%), and October (n = 2; 50%). We captured 11 gravid females from July to October 2011, and 12 from June to October 2012. An additional gravid female used in this study was collected opportunistically in May 2011 prior to the start of structured surveys. During July 2011 to October 2012, all collected gravid females (n = 24) oviposited during June (n = 3), July (n = 4), August (n = 10), September (n = 2), and October (n = 5). Only a single clutch was recorded for each female included in this study.

Clutch data

We collected egg and clutch data from 24 gravid female Oustalet's Chameleons. A total of 1014 eggs (mean = 42 ± 11.76; range = 17–72) were laid. Gravid females averaged 164 ± 1.53 mm SVL (*n* = 14) with a mean post-capture mass of 124.0 ± 35.8g (*n* = 12) (Table 1). Mean egg dimensions among 15 clutches were 16.7 ± 1.3 mm x 10 ± 0.88 mm (*n* = 149). Artificially incubated clutches (*n* = 4) began hatching after 285–354 days, and all viable eggs (59–93% of each clutch) hatched within 21 days of the first hatching from their respective clutches. Clutch size relative to female SVL (*n* = 14) was not significant ($R^2 = 0.20$; $P = 0.06$; Fig. 3), while clutch mass and female mass (*n* = 9) were significantly correlated ($R^2 = 0.49$; $P = 0.04$; Fig. 4).

In situ nesting

We released the female chameleon outfitted with a radio transmitter at the point of capture and began tracking on 17 October 2013. She stayed in the same tree for 6 d, and then we tracked her to the base of an Avocado tree 42 m west of the initial capture and release site. We found 2 open cavities in the substrate at the base of the Avocado tree where she was tracked. Avocado trees at this site are planted in large, elevated soil mounds because of the solid limestone substrate in southeastern Florida. The opening of the larger of the 2 cavities was on the southern side of the Avocado tree facing southward. The cavity entrance was 9 cm wide and the egg closest to the nest-chamber entrance was at a depth of ~42 cm from the cavity opening. Upon further excavation, we found the chamber to be ~6 cm wide and 23 cm long. The chamber contained 58 eggs scattered throughout; some were partially buried by substrate. The clutch weighed 60.2 g, with a mean egg length of 17.2 ± 0.93 mm (*n* = 13, range = 16–19 mm) and width of 10.4 ± 0.51 mm (*n* = 13, range = 10–11 mm). We measured the temperature and relative humidity of the interior chamber to be 27.2 °C and 94.9%, respectively. Ambient air temperature was 27.3

Table 1. Individual, clutch, and egg morphometric data for gravid female Oustalet's Chameleons collected in Florida 2011–2012. *n* = sample size for egg dimension data.

ID	Capture month and year	SVL (mm)	Post-capture mass (g)	Oviposition month and year	Clutch size	Clutch weight (g)	Mean egg length (mm)	Mean egg width (mm)	*n*
67	July 2011	162	105	July 2011	32	-	-	-	-
69	July 2011	158	75	August 2011	39	36	16	10	10
95	July 2011	164	110	August 2011	49	30	15	8	10
118	August 2011	160	120	August 2011	47	-	-	-	-
122	August 2011	170	110	August 2011	35	36	18	9	10
127	August 2011	165	110	August 2011	34	26	16	9	10
149	October 2011	140	100	October 2011	39	38	16	11	10
310	June 2012	145	92	June 2012	42	30	17	11	6
312	June 2012	195	188	June 2012	62	76	16	11	10
327	June 2012	165	130	July 2012	49	49	15	9	10
328	June 2012	182	170	July 2012	44	50	19	10	10
397	August 2012	145	-	August 2012	41	46	17	10	10
410	August 2012	165	-	August 2012	35	39	18	10	10
427	October 2012	184	178	October 2012	58	-	-	-	-

°C with 94.9% relative humidity. We could not determine if the female dug these cavities or utilized some that were already present. After data collection, we removed and discarded the eggs from this clutch to preempt hatching.

Discussion

Our study provides the first documentation of natural reproduction in Oustalet's Chameleon in Florida, as well as a description of a nesting site and a new maximum clutch size. Little information has been published on chameleon natural history (see Herrmann and Herrmann 2005, Measey et al. 2014, Reaney et al. 2012), especially related to reproduction and oviposition in wild populations. Published data suggest that oviposition for chameleons occurs during the summer months, when rains are at or near their peak (Andrews and Karsten 2010, Cuadrado 1999, Herrmann and Herrmann 2005, Karsten et al. 2008, Reaney et al. 2012; Table 2). Our data support this premise, including our observed oviposition by wild-collected gravid female Oustalet's Chameleons that oviposited from June to October, which are the summer and rainy-season months in Florida. However, stress from capture and handling or husbandry variations could have caused early or delayed oviposition.

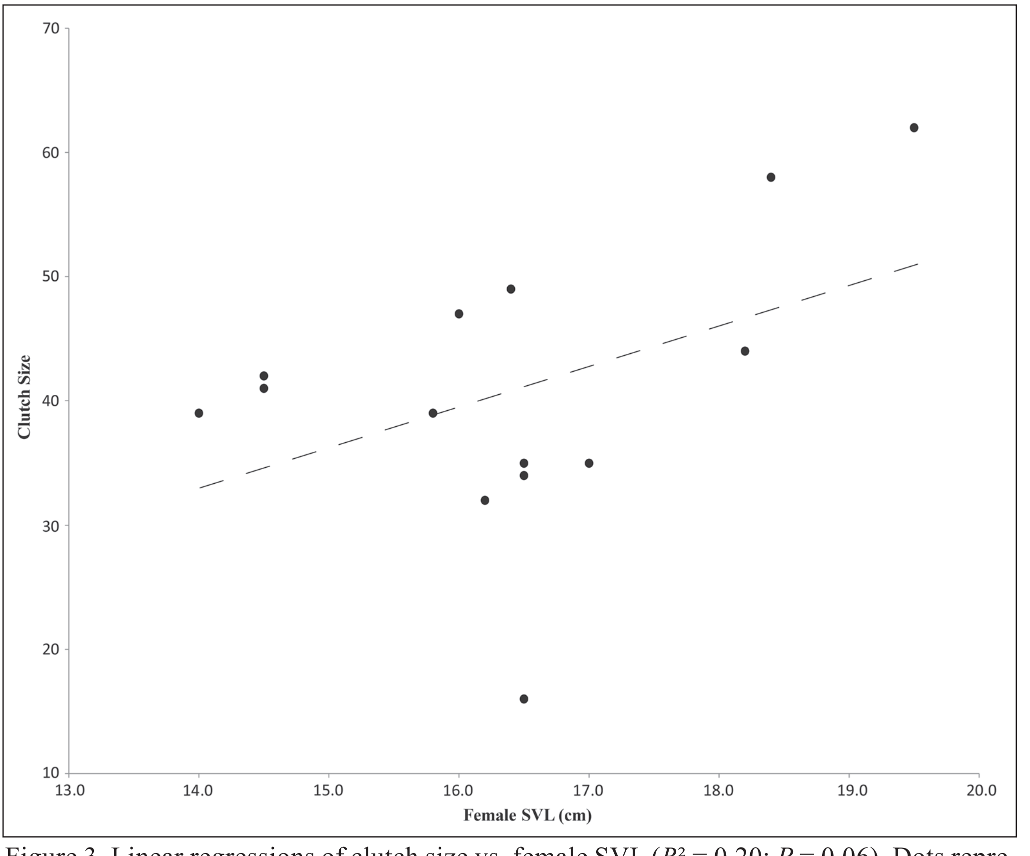

Figure 3. Linear regressions of clutch size vs. female SVL ($R^2 = 0.20$; $P = 0.06$). Dots represent individual clutch data from separate females. The dashed line depicts a non-significant relationship.

Chameleons are known to reproduce seasonally or continuously throughout the year, depending on biotic and abiotic factors, with seasonally reproducing chameleons often ovipositing prior to winter and having long incubation lengths that include diapause (Measey et al. 2014). Chameleons may have adapted and extended the timing of breeding and nesting seasons in regions with stable temperatures and highly seasonal rainfall (Shine and Brown 2008). Avoidance of nest and offspring predation may also contribute to an extended nesting period (Jackson 1988). The reproductive phenology for Oustalet's Chameleon is unknown, but our data, including the pre-winter oviposition and an extended incubation length, suggest that there may be an extended, seasonal reproduction season in southeastern Florida. Although the incubation lengths we observed may be biased because of captive-temperature stability or lower incubation-temperatures, incubation time is extended for the species. Environmental factors contributing to this extended, seasonal reproduction season may be the subtropical climate with moderate year-round temperatures and seasonal precipitation. As in other lizard species, a major contributing factor to seasonal reproduction in Oustalet's Chameleon may be availability of prey for offspring (Fitch 1982).

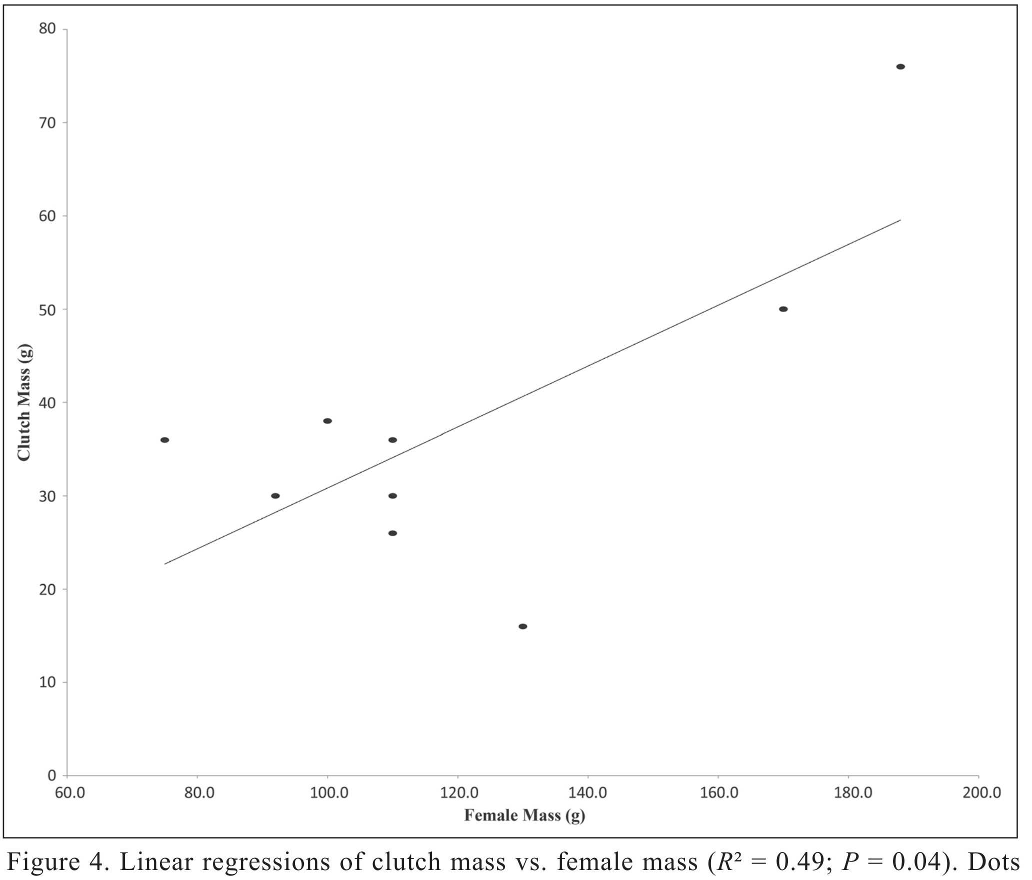

Figure 4. Linear regressions of clutch mass vs. female mass ($R^2 = 0.49$; $P = 0.04$). Dots represent individual clutch data from separate females. The solid line depicts a significant correlation.

Clutch sizes vary greatly among chameleon species. Clutch sizes tend to increase with increasing SVL (Andrews and Karsten 2010), but this relationship can vary both interspecifically and intraspecifically (Table 2; e.g., Andrews et al. 2008, Burrage 1973, Nečas 2004, Reaney et al. 2012). Unlike patterns among some other chameleon species, such as *Chamaeleo chamaeleon* (L.) (Common Chameleon) and interspecific relationships (Andrews and Karsten 2010, Cuadrado 1998), we did not observe a correlation between clutch size and female SVL (Fig. 3). This difference may be due to the more limited range of body sizes in our analysis relative to other studies, small sample size, or the influence of an outlier (see Fig. 3). In addition, we found a positive correlation between female mass and clutch mass (Fig. 4). The results of both our clutch size vs. female SVL and clutch mass vs. female mass correlations may be strengthened by additional sampling, particularly among larger females.

Oustalet's Chameleon was previously known to have a maximum clutch size of 61 eggs (Brygoo 1971, Glaw and Vences 2007, Nečas 2004, Spawls et al. 2002), however 2 females in our study laid clutches of 62 and 72 eggs, respectively. Incubation time for this species at a constant 28 ºC is known to range from 210 to 280 d (Nečas 2004), but we found that clutches can incubate at a much lower temperature range (19–23 ºC) and still remain viable. However, incubation at lower temperatures leads to considerably longer incubation times to hatching (285–354 d), ~75 d longer than reported by Nečas (2004). These findings illustrate a high reproductive potential for this species, and egg resilience to a wide range of incubation temperatures.

Utilizing radio telemetry to detect nesting locations of nonnative species has been successful in southeastern Florida. In addition to our study, other radio-telemetry studies have been able to find nesting locations for other invasive reptiles in Florida including *Salvator merianae* A.M.C. Duméril & Bibron (Argentine Black and White Tegu; Pernas et al. 2012) and *Python molurus bivittatus* Kuhl (Burmese Python; Snow et al. 2007). Based on our tracking efforts with Oustalet's Chameleon and the temporal presence of gravid females, oviposition likely occurs from June to October. Additional studies are needed to confirm in situ locations of nests to determine if Oustalet's Chameleon uses locations for oviposition sites other than Avocado tree mounds.

This population of Oustalet's Chameleon in southeastern Florida was intentionally released in this privately owned Avocado grove (Gillette et al. 2010), possibly for the same reason the *Trioceros jacksonii xantholophus* (Eason et al.) (Jackson's Chameleon) release locations were chosen in Hawaii. Jackson's Chameleons were released near *Mangifera indica* L. (Mango) and *Psidium guajava* L. (Guava) trees because the fruit attracts fruit pests that are also prey for neonates (Kraus et al. 2011). Jackson's Chameleons were then spread throughout the island and were eventually sold in the pet trade. It is unclear if Oustalet's Chameleon and other chameleon species are being spread in a similar manner in southeastern Florida, although it seems likely (Edwards et al. 2014). Agricultural lands in this area provide fruit that attracts prey, which would be immediately encountered by neonates hatching at the base of fruit trees. Most natural areas of Miami-Dade County have

Table 2. Interspecific comparison of reproductive traits and associated ecological factors of 6 oviparous chameleon species.

Species	Location	Female SVL (mm)	Clutch size Range (mean)	Oviposition months (season)	Incubation length	Hatching months (season)	References
Chamaeleo chamaeleon L. (Common Chameleon)	Southern Europe	87–135	6–28 (12)	Sep–Oct (summer/ early rainy)	10.5–12 mo	Aug–Nov (summer/rainy)	Andrews et al. 2008, Cuadrado 1999
Trioceros montium (Buccholz) (Cameroon Sailfin Chameleon)	Southwestern Cameroon	65–90	3–12 (6.5)	Feb–Jun (summer/ early rainy)	~3.5 mo (in lab)	~May–July (summer/rainy)	Hermann and Hermann 2005
Chamaeleo dilepis Leach (Common Flap-necked Chameleon)	Southern Africa	>80 mm	19–74 (44.2)	Nov–May (summer/ early rainy)	-	-	Reaney et al. 2012
Furcifer labordi (Grandidier) (Laborde's Chameleon)	Madagascar	-	-	Jan–Mar (mid-late summer/ mid-late rainy)	8–9 mo	Nov–Dec (early summer/ early rainy)	Karsten et al. 2008
Chamaeleo namaquensis Smith (Namaqua Chameleon)	Namibia	90–143	6–22 (11.8)	May–Oct (winter–spring/ rainy)	91–112 d	Sep–Jan (spring–summer)	Burrage 1973
Furcifer oustaleti Mocquard (Oustalet's Chameleon)	Southeastern Florida	145–195	17–72 (24)	Jun–Oct	285–354 d (summer/rainy)	Jul–Oct (summer– early fall)	This study

a solid limestone substrate (Hoffmeister et al. 1967) in which it would be difficult for Oustalet's Chameleon to excavate a nest. The disturbed and enhanced soil mounds and irrigation systems in Avocado groves provide adequate nesting sites for chameleons and provide proper soil, moisture, and humidity throughout the year. This combination likely provides Oustalet's Chameleon a greater chance for survival, reproductive success, and population persistence compared to native habitats. Because of these factors, disturbed areas, such as agricultural or urban areas may be suitable for some non-native lizards. The most widespread, introduced chameleon in Florida is the Veiled Chameleon. It is established in at least 3 counties (Enge 2008, Gillette and Krysko 2012, Krysko et al. 2004, Meshaka 2011) where it thrives in agricultural areas and anthropogenically altered habitats similar to the one reported herein. Although we are not aware of chameleons that have colonized any natural areas in Florida, there have been other non-native reptiles that thrive in natural areas. In southeastern Florida, the Argentine Black and White Tegu was first observed in an agricultural area, and has been seen in a variety of disturbed and natural areas (Pernas et al. 2012). Some of these sites also have disturbed mounds of soil, which may provide suitable nesting sites and contribute to persistence of new populations.

It is unclear if Oustalet's Chameleon has a negative impact on native species, but this species shows similar characteristics to other established nonnative species. Lizards are the most successful nonnative reptile taxa in Florida, and they share many traits including high fecundity and early maturation (Meshaka 2011). Successful nonnative species also tend to have widespread native ranges, abundant populations, and adapt well to climates outside of their natural range (Sakai et al. 2001, Williamson and Fitter 1996). Oustalet's Chameleon is fecund, having clutch sizes of 17–72 eggs with offspring becoming sexually mature in 1 y (Glaw and Vences 2007; D. Smith et al., unpubl. data), and occurs in a variety of habitats throughout much of Madagascar (Glaw and Vences 2007). In 1 survey of a dry deciduous forest in northern Madagascar, Oustalet's Chameleon was the most common reptile encountered (Labanowski and Lowin 2011). Based on climate data from 2005 to 2015 at the Antsiranana Airport weather station in northern Madagascar, the mean annual temperature there is 25.4 ºC (range = 12.2–32.4 ºC). This temperature is very similar for the same range of dates in southeastern Florida at the Miami International Airport weather station where the mean annual temperature was 25.1 ºC (range = 1.6–35.5 ºC); the range is wider and the minimum temperature is lower. We assume that this species has adapted to the climate of southeastern Florida, as it has been at this Avocado grove for more than 10 y (Gillette et al. 2010).

Knowledge gained from our study can aid in the management of Oustalet's Chameleon and other introduced species. Removal of reproductive individuals is a key component in the eradication of an invasive species (Bomford and O'Brien 1995). Based on knowledge of the reproductive season, removal efforts can be intensified during that time. Because we encountered gravid females from June to October and the majority of females oviposited in August, removal during these months, with efforts peaking by the end of July, would be the most effective at reducing population growth. Although removal of the reproductive population is crucial, it is as important to diligently study invasive species during the removal process to learn about their biology. It is also imperative to create a management plan for removal, and consistently survey until the population is eradicated.

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