SHORT COMMUNICATION

Winter aggregation in *Anolis equestris* and *A. lucius* (Squamata: Dactyloidae), two territorial species from Cuba

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Organisms tend to aggregate to increase survival and reproduction in response to poor environmental conditions and/or limited availability of resources (Stamps 1988, Bishop and Echternacht 2004, Rabosky et al. 2012). Usually such factors are patchily distributed in both space and time (Elfström and Zucker 1999, references therein, Begon et al. Aggregation in reptiles may occur in response to nesting, reproduction, sleeping, thermoregulation, and hibernation (Boykin and Zucker 1993, Graves and Duvall 1995, Elfström and Zucker 1999, and references therein). Temperature is the most important parameter influencing thermoregulation and hibernation. It is more critical to the activities of ectothermic organisms than endothermic ones (reviewed in Huey and Berrigan 2001, Vitt and Cadwell 2014) because ectotherms have inefficient physiological mechanisms to thermoregulate. Thus, ectotherms have developed alternate mechanisms (e.g., behavioral thermoregulation) to maintain a given temperature (Huey and Kingsolver 1993). Temperature variation can be a key factor in driving the rapid transition from solitary to social behavior, especially in ectotherms (Rabosky et al. 2012), if the social behavior leads to a better thermal condition. The better thermal condition can be limited to a small area in which the individuals choosing the most thermally suitable sites can increase their survival (e.g., Distler et al. 1998), thereby leading to the social behavior of aggregation.

Winter is the most critical time of the year for survival of ectotherms (reviewed in Elfström and Zucker 1999) and winter aggregation has been reported in snakes, turtles, and several lizard species (reviewed in Bishop and Echternacht 2004). Although this strategy may

Received 21 December 2015 Accepted 12 September 2016 Distributed December 2016 occur for a variety of reasons, a low availability of over-wintering sites and thermoregulation repeatedly have been suggested to be critical (Bishop and Echternacht 2004, Winck and Cechin 2008).

Because species of Anolis are highly territorial, aggregation in this group of lizards is rare (Losos 2009). Males usually are territorial to other males, especially during the breeding season, and females frequently are territorial to all individuals of a similar size, including males and occasionally heterospecific anoles the whole year (Rand 1967, Stamps and Crews 1976, Stamps 1977). Aggregation in anoles can involve territory overlap (i.e., male territories encompass the territories of several females) and communal nesting (Henderson and Powell 2009, Losos 2009, Robinson et al. 2014). As Anolis is almost exclusively Neotropical (Nicholson et al. 2012), winter aggregation in these lizards has been reported only in the northernmost U.S. populations of Anolis carolinensis Voigt, 1832 from Georgia (Neill 1948), South Carolina (Distler et al. 1998), and Tennessee (Bishop and Echternacht 2004). The aggregations can occur under logs, and in stumps and rock crevices (Hamilton 1948, Neill 1948, Bishop and Echternacht 2004 respectively) where as many as 29 individuals have been found in the same stump (Neill 1948). Aggregations have been found at localities characterized by a continental subtropical wet climate that includes nocturnal temperatures near freezing in winter with occasional snowfall, and temperatures may drop below freezing and persist for several days (Distler et al. 1998). Heterospecific winter aggregation was reported by Hamilton (1948) who saw two specimens of A. carolinensis and five of the scincid Plestiodon fasciatus (Linnaeus, 1758) (referred therein as Eumeces fasciatus) at a temperature of 2.2°C in Grant County, Louisiana, in late January. Thus, winter temperatures may be a limiting factor in the northern distribution of A. carolinensis (Distler et al. 1998).

Herein we report winter aggregation in two species of anoles from northwestern Cuba. This

is the first record of aggregation behavior in a tropical anole species. At 11:16 h, on 08 February 2009, we found eight adult forestdwelling crown-giant anole (Anolis equestris buidei Schwartz & Garrido, 1972) aggregated in a rustic wooden construction (typical Cuban construction called ranchón) at the Varahicacos Protected Area (23°11'38" N, 81°09'00" W; datum WGS 84) on the Hicacos Peninsula, the northernmost point of mainland Matanzas Province. The animals were resting, eyes-closed, and in dark phase coloration on rafters about 4 m above the ground in the roof of the building. They remained immobile while we observed and photographed them. The lizards were resting adjacent to one another, with some individuals almost in contact (Figure 1A); they occupied an area less than 4 m² beneath the roof. We did not observe any active lizards outside of the building during this visit. Interviews with local workers revealed that this behavior occurs annually during the cooler months. The nearest weather station (Varadero, Matanzas Province, 12 km Varahicacos) recorded the temperatures between 2009 and 2011 from December-March, when average temperatures ranged from 17.1–22.3°C (data provided by the archive of the Instituto de Meteorología of Cuba at the request of authors). Although A. equestris buidei occasionally is observed inside the same building during warmer months, we observed individuals more frequently on trees around the building by day and night, when lizards were sleeping. Indeed, during two additional visits on 01 July 2009 and between 10-13 April 2015, we did not see any lizards inside the building, but did observe four and five individuals. respectively, in an area of about 60 m² around this building. During the July and April visits, the lizards were in light phase when active by day (Figure 1B) and while sleeping at night on terminal branches of the trees.

We observed a second winter aggregation at 16:25 h on 14 December 2012 during an expedition to the mouth of the Río Jaruco in the municipality of Santa Cruz del Norte, Mayabeque

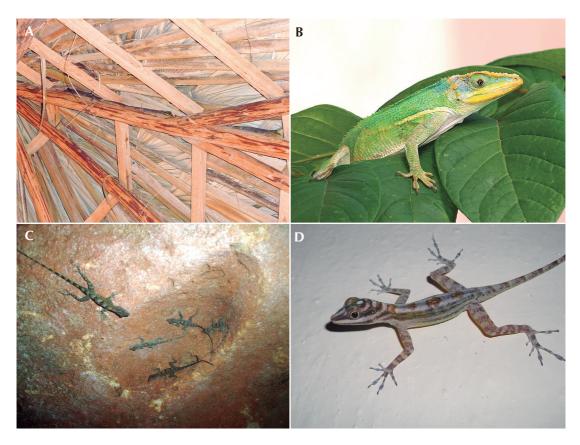


Figure 1. (A) Anolis equestris buidei aggregated inside a ranchón at Hicacos Peninsula, Matanzas, Cuba. Three specimens can be observed, all in dark phase. (B) Anolis equestris buidei in light phase. (C) Anolis lucius aggregated in a roof depression inside a cave nearby Jaruco River, Mayabeque, Cuba, all in dark phase. (D) Anolis lucius from Banao, Sancti Spiritus, Cuba, in light phase. Photographs A and D by Javier Torres, B by Raimundo López-Silvero, and C by Carlos A. Martínez Muñoz.

Province. Five individuals of the rock-dwelling anole, *Anolis lucius* Duméril & Bibron, 1837, were aggregated in a roof depression of less than 1.5 m² (Figure 1C) at the entrance of "Cinco Cuevas" cave (23°10'14" N, 82°00'17" W; *datum* WGS 84). This cave is of phreatic origin, opens in a fossil marine terrace, and has a complex system of interconnected chambers and galleries (Núñez-Jiménez 1967). Owing to its several entrances, there is a constant air circulation through the cave. The air temperature inside the cave was 20.5°C. We could not measure the

temperature of the substrate on which the lizards were found, but it seemed warmer than the air temperature; the ventral surface of each of the lizards was in contact with the substrate and the lizards were in a dark color phase (Figure 1C). Thus, it is possible that they were thermoregulating by thigmothermy (i.e., thermoregulation by direct contact with a preheated surface, Wareham 2005). When active, anoles usually are in a light color phase (Figure 1B, D).

Like many other reptiles, anoles usually are largely solitary and territorial, especially during the breeding season (Losos 2009). But aggregation, particularly during cooler months, might be more common than the few literature reports suggest. The reasons for such aggregations remain unclear, although the case reported herein can be classified as a temporary, condition-based aggregation (suitable temperature as limiting factor) (Graves and Duvall 1995) that may reflect the lizards' preference for relatively warmer microclimates. Even though winter temperatures in Cuba are never freezing, the areas where we observed the lizards have some of the coldest winter temperatures on the island, frequently below 5°C (Institute of Meteorology of Cuba). Aggregation of individuals in contact may further reduce heat loss in reptiles (Myers and Eells 1968, Boersma 1982); however, some winter aggregations reported in A. carolinensis (Bishop and Echternacht 2004) and the aggregations reported here involved several individuals in close proximity but not huddling. Alternately, loss and fragmentation of forested areas at the Península de Hicacos (Torres et al. 2014) may have reduced natural over-wintering sites for Anolis equestris buidei, forcing lizards to leave their natural habitat and aggregate in buildings in search of better thermal conditions.

The close proximity of individuals in both of the aggregations suggests that some factors determining territoriality in other periods of the year (i.e., availability of potential mates, food and basking perches; reviewed in Stamps 1977), are secondary when temperature is not suitable. Another factor that may enhance aggregating behavior is the tendency of males to be less territorial during the non-breeding season, when sometimes they overlap the territories of several females and even those of smaller males (Andrews 1971, Fleming and Hooker 1975). Moreover, females of some anole species are highly territorial year-round, because the main factor determining such territoriality is food (Schoener and Schoener 1982, Jenssen et al. 1998). The overlap in females' territories is larger than that of the males (Losos 2009); nevertheless, individual anoles are separated

from one another, in contrast to out observations of some individuals being nearly in contact with one another.

According to the thermal melanism hypothesis, dark coloration is advantageous under lowtemperature conditions in heliothermic species (Clusella-Trullas et al. 2007 and references therein). This hypothesis is relevant to anoles, which are diurnal, and alternate dark and light color phases to thermoregulate (Angilletta 2009). When anoles need to warm up by heliothermy they may asssume a dark color phase (Campbell 1971). At night, when temperatures are lower and activity is minimal (because they are sleeping), anoles are in light phase (see Figure 10.7 in Losos 2009). They also are in light phase when there is no need to warm up because heat is not limited as, for example, during the midday (Rodríguez et al. 2010). The dark color phase is related to behavior (e.g., during territorial displays males tend to change to dark phase) and thermoregulation (to gain heat from sun radiation individuals change to dark phase) (see Figure 9.4 in Losos 2009, Rodríguez et al. 2010).

The dry season in the tropics is cooler than the wet season, and typically, more limited in food and water resources (Institute of Meteorology of Cuba, Wolda 1980, Tanaka and Tanaka 1982, Iturriaga and Marrero 2009). Maintaining the dark phase is energetically more demanding than keeping the light phase, because the former requires movement of cromatophores (Riley 1997, Talloen et al. 2004). We assume that when anoles maintain a dark phase, it probably is more critical to gain heat than to obtain food. In this case, dark phase seems to be linked to thermoregulation, because all aggregated anoles were dark. In contrast, specimens from the same locality and observed at the same time each day but in a different season (wet vs. dry, hot vs. cool respectively) were in a light color phase color.

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