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RESEARCH

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First description of courtship and copulation in *Pristidactylus casuhatiensis* (Squamata, Leiosauridae)

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Abstract

Background Reproductive behaviour under natural conditions is hard to record, especially in rare and cryptic species, such as the Casuhatien anole (*Pristidactylus casuhatiensis*). This medium size lizard is endemic to the Sierras Australes Bonaerenses, a rocky outcrop in the Southern Pampas of Argentina.

Methods During spring and summer from 2018 to 2022, we surveyed five hills at above 600 m altitude, where specimens were known to occur. Every time we detected a courtship or copulation event, we took photographs of the specimens for their individual identification, and recorded the body temperature of the participating individuals as well as air temperature, wind speed and relative humidity. We recorded the duration in minutes of each phase of the event (immobilization, juxtaposition of the cloacae followed by copulation, and finally, restraint and separation) and described the main habitat features of the site where it happened.

Results We detected 12 reproductive events; all of them occurred in October and November, on Funke, Puntudo and Tres Picos hills, mostly between 1300 and 1700 h. The mean duration of each copulation phase was 6 min (95% CI = ± 1.4, $n = 10$), 4.3 min (95% CI = ± 1.8, $n = 10$) and 3.8 min (95% CI = ± 3.42, $n = 10$), respectively.

Conclusion The reproductive activity of the Casuhatien anole is concentrated in the spring, particularly in the early afternoon, following the patterns described for other species of lizards. During these events, the greatest exposure of individuals could make them more vulnerable. This, together with other features related to their reproductive behaviour revealed in this paper may contribute to the planning of conservation actions.

Keywords Behaviour, Endangered, Endemic, Leiosauridae, Lizards, Pampas grasslands, Reproduction

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Background

Observations of reptile behaviour under natural conditions are rare and data collection is challenging, especially for occasional events such as courtship and mating [22, 39]. Saurian courtship involves a variety of actions performed by males and females prior to copulation [10]. In diurnal lizards, the use of characteristic postural movement-based signals by males may facilitate mate attraction by increasing visibility, encoding individual identity, and advertising quality [28, 45, 47]. Most scaly reptiles are promiscuous and there is no parental care after hatching [27]. In territorial species, males may occupy areas that typically include the home ranges of several females,

leading to a polygynous mating system. This system commonly occurs in lizards, whose males often move around actively seeking mates [7, 32]. Copulation includes three phases: immobilization of the female by the male, copulation (juxtaposition of cloacae) and finally restraint and separation [35, 40]. If the female is receptive, copulation occurs when the male stands over her, orienting his pelvic region to bring their cloacae into contact, and inserts one of his hemipenis into the female's cloaca [34].

The genus *Pristidactylus* comprises 10 species, six of which are native to Argentina. They distribute from 31°S in Argentina and Chile to central Argentine Patagonia [20, 23]. Individuals are difficult to find due to their secretive behaviour [12]. Some of the species have a disjunct and restricted distribution [21]. This is the case of the Casuhatien anole (*Pristidactylus casuhatiensis*, locally known as iguana de cobre), which is endemic to the Ventania Mountains [12]. With a maximum elevation of 1234 m, this mountain system includes the highest peaks of the Argentinean Pampean ecoregion. The Casuhatien anole occurs on hilltops above 600 m, associated with rocky surfaces, crevices and low grasslands. They are diurnal, medium sized, cryptic and sexually dichromatic, with males having a greenish dorsal coloration and a yellowish ventral and lateral region, and females having a brownish dorsal coloration and a whitish lateroventral region [11, 14]. Their colours become more intense as the animals increase their exposure to the sun (Lujan Ogeda and Areco, pers. obs.). Due to its limited distribution, low numbers and the threats it faces, the species is critically endangered [16]. Based on our previous observations, these specimens are active during the warm and humid months (October to April) and hibernate during the cold and dry season (May to September), following typical patterns seen in lizards in temperate regions. Low temperatures can limit their activity, especially for breeding (Adolph and Porter [1], in [30]. In this study, we describe for the first time the courtship and copulation behaviour of *Pristidactylus casuhatiensis*, which in turn is the first description of this behaviour under natural conditions for the entire genus. We looked for differences in air temperature at the time of copulation depending on the copulation site (sun, shade or sun-shade), and also in the body temperatures of males and females during the copulation phases.

Methods

During the spring and summer of 2018–2022, we carried out 128 field surveys, for a total of 441.8 h, in the five hills where the species is known to occur: Funke (-38.08935, -62.07214; 656 m altitude), Napostá (-38.15731, -61.95171; 1090 m altitude), Puntudo (-38.12253, -6197760; 850 m altitude) and Tres Picos (-38.15731, -61.95171; 1234 m altitude), at Estancia Rodolfo Funke, and Cerro Ventana (-38.04837, -62.01873; 1034 m altitude), at Ernesto Tornquist Provincial Park, all in the Tornquist District, Province of Buenos Aires, Argentina (Fig. 1). We recorded all reproductive events and identified the individuals involved by photographing and then analysing the pattern of spots on the sides of their heads (Areco Anibal, Dept. of Protected Areas, Buenos Aires, unpublished data). We also recorded the exposure of the animals to the sun or the shade during courtship and copulation. We measured the duration of each copulation phase and recorded the body temperature (°C) of each male and female using a hand-held Xueliee Lasergrip GM320 laser-infrared thermometer (Shandong Aoyoo CNC Equipment Co., Ltd.). We also recorded air temperature (°C), relative humidity (%) and mean wind speed (km/h) using a hand-held digital anemometer, model TL-302 (Dongguan Xinrui Instrument Co., Ltd.). We photographed and videotaped the sequence of courtship and mating events using a Sony HX400V digital camera (Sony Group Corporation) and described behaviours according to Carpenter and Ferguson [9] and Carpenter [10]. We report all mean values ± 95% CI.

Since our data did not fit a normal distribution, we used Kruskal–Wallis test to compare mean air temperatures between encounters in sunny and shady sites, and when animals moved from a sunny place to the shade, and to look for differences in mean body temperatures of males and females during copulation. We performed the analyses in R 4.2.0 [36] with a significance level of $\alpha = 0.05$.

Results

We recorded 12 courtships and mating encounters involving five males and eight females. All events took place in October and November and we only observed them on the hills of Funke, Puntudo and Tres Picos, mostly between 13:00 and 17:00 h (Table 1). Four pairs repeated their copulations: one on the same day, an hour and a half apart; another in successive months of the same year; and the last two in successive years (Table 1). Courtship and subsequent copulation had a total duration of 16.91 min (95% CI = ± 6.91, $n = 11$). We identified three phases during copulation: immobilization, copulation (juxtaposition of the cloacae), and finally, restraint and separation. The duration of each phase was 6 min (95% CI = ± 1.4, $n = 10$), 4.3 min (95% CI = ± 1.8, $n = 10$) and 3.8 min (95% CI = ± 3.42, $n = 10$), respectively. All copulations took place in rocky environments. Some of them occurred in the shade (41.66%) within or close to a crevice in the rocks; in 33.33% of the cases, copulation started in the sun and then the animals moved to a shady place, while in the remaining 25% the whole sequence took place in the sun. Air temperature during the events

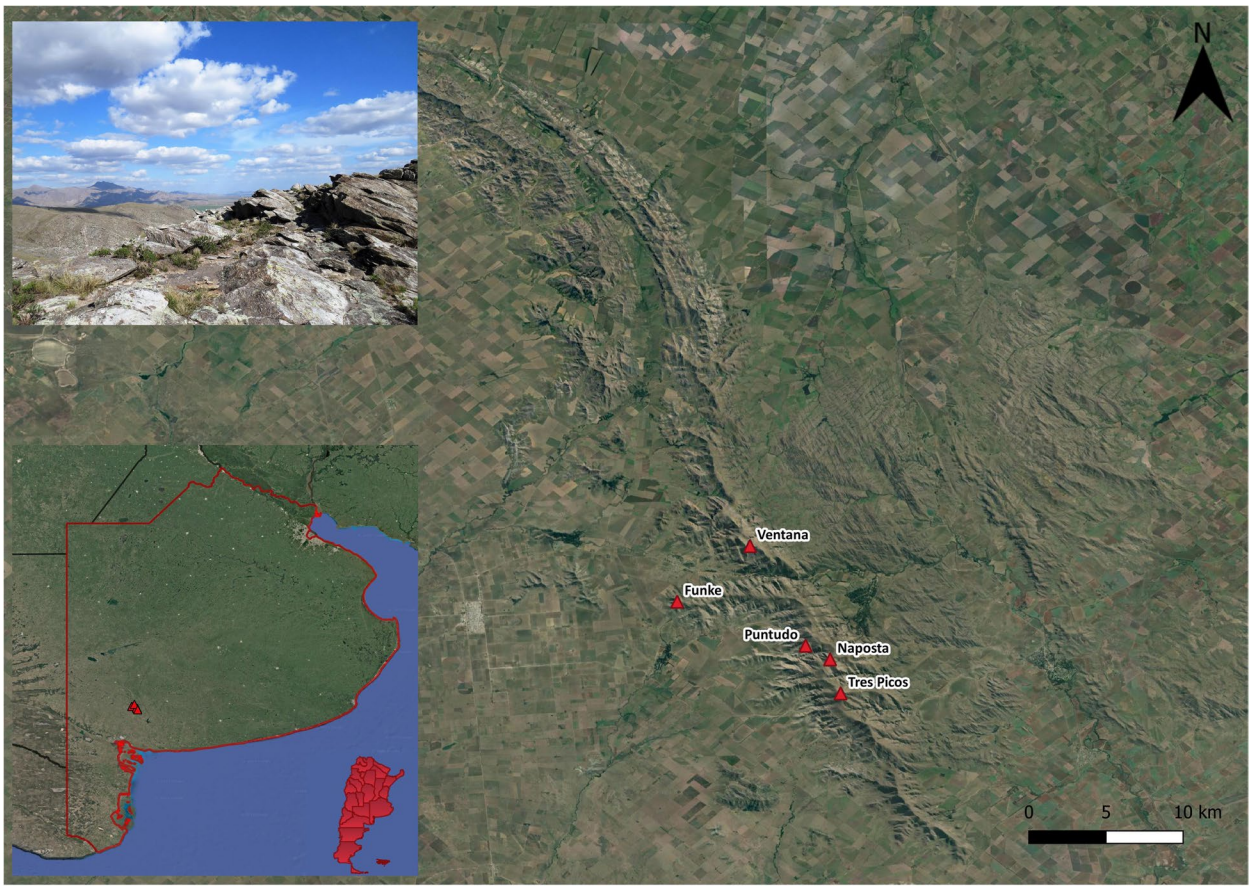

Fig. 1 Location of the mountain range where reproductive behaviour of *Pristidactylus casuhatiensis* was recorded, Ventania System, Buenos Aires province, Argentina

Table 1 Casuhatien anole (*Pristidactylus casuhatiensis*) copulation events recorded in the hills of the Ventania system, Buenos Aires, Argentina, between 2018 and 2022. 1st phase- immobilization, 2nd phase- copulation (juxtaposition of the cloacae), and 3rd phase- restraint and separation

Date	Site	Start time	Male id	Female id	Total duration	1st phase	2nd phase	3rd phase
3 Nov 2018	Funke	1435 h	M7	H2	45	-	-	-
19 Oct 2019	Funke	1405 h	M5	H3	25	10	5	10
29 Oct 2019	Funke	1215 h	M5	H4	10	5	3	2
31 Oct 2019	Funke	1129 h	M5	H1	12	5	4	3
19 Nov 2019	Funke	1540 h	M5	H3	21	3	2	16
23 Oct 2020	Tres Picos	1400 h	M4	H7	-	-	-	-
28 Oct 2020	Funke	1540 h	M5	H4	27	8	12	7
6 Nov 2020	Funke	1054 h	M5	H1	5	3	2	0
27 Oct 2021	Puntudo	927 h	M14	H10	10	7	3	0
27 Oct 2021	Puntudo	1057 h	M14	H10	9	6	3	0
27 Oct 2021	Puntudo	1319 h	M13	H9	12	8	4	0
20 Nov 2021	Puntudo	1357 h	M14	H11	10	5	5	0

was 27.43 °C (95% CI = ± 3.15). We found no significant differences in air temperature when copulation took place in the sun or in the shade, or for animals starting courtship in the sun and then moving to the shade (H = 2.0455, df = 2, $P = 0.359$, $n_{sun} = 2$, $n_{shade} = 4$, $n_{sun\text{-}shade} = 4$). Mean body temperature at copulation was 25.14 °C (95% CI = 3.12) for males and 26.31 °C (95% CI = ± 1.98) for females, with no significant differences between them (H = 6.6667, df = 6, $P = 0.3528$, $n_m = 8$; $n_f = 10$). Relative humidity during copulation was 20.61% (95% CI = ± 4.68) and wind speed was 7.55 km/h (95% CI = ± 3.92).

Our observations started with the individuals at a mean distance of 3.88 m (95% CI = 1.29, Fig. 2), and with the males approaching the females. On several occasions, males displayed behaviours that made them more visible, including push-ups, head bobbing and rapid tongue flicks over the ground. When both individuals were in close proximity, the male tried to grab the female by biting some part of her dorsal region until his mouth reached her neck or shoulder (Fig. 3A). Some males maintained the behaviour of rapid tongue protrusion and retraction, in this case over the dorsal region of the female's body. The female often attempted to free herself by slightly arching her neck and slowly and periodically waving her forelimbs (waving behaviour). These behaviours correspond to the immobilization phase. Finally, after several attempts, the male sought the best position for copulation by placing one of his hind limbs around the female's abdomen, while continuing to hold her with his mouth (Fig. 3B). The male then turned his body to contact both cloacae (Fig. 3C); At this point he inserted one of his hemipenes and performed rhythmic pelvic contractions, indicating ejaculation. An accompanying phase was observed in 50% of the cases, without cloacal contact, but with the male still immobilizing the female with his bite (Fig. 3D), whereas the other 50% separated immediately after copulation and each participant moved in a different direction.

During three reproductive events, we heard sounds that resembled the hissing described for other leiosaurid species [17, 18]. In the first case, we hear it coming from a couple that has just copulated. In the second case, it was produced before copulation began. In neither case we were able to record any other behaviour associated with the sound, as the animals moved to sheltered areas between the rocks. We observed the last case in detail, which involved a pair where the male approached the female and triggered her rejection behaviour. The male attempted to approach the female while she had her tail

Fig. 2 Breeding pair of the Casuhatien anole (*Pristidactylus casuhatiensis*) in the Ventania system (Buenos Aires, Argentina). Moment before copulation. The female is on the left and the male on the right

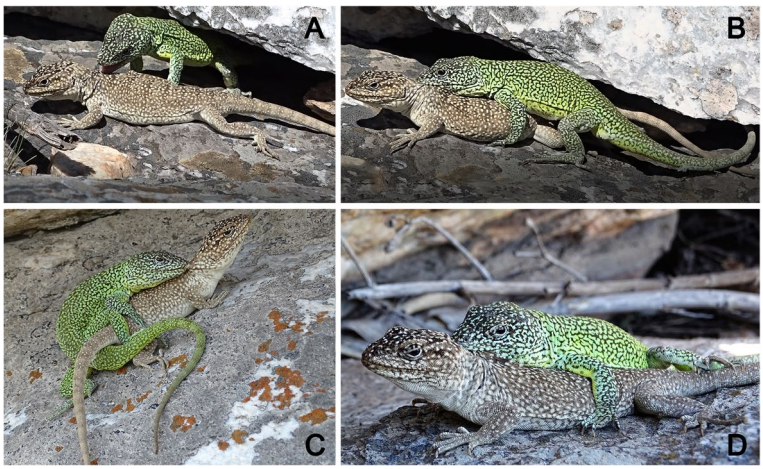

Fig. 3 Phases of copulation of the Casuhatien anole (*Pristidactylus casuhatiensis*) in the Ventania system (Buenos Aires, Argentina). **A** and **B** 1st phase: immobilization, **C** 2nd phase: copulation (juxtaposition of cloacae), **D** 3rd phase: restraint and separation

oriented to the male. When the male was in front of her, the female arched her back, lowered her head, inflated her abdomen, and made the above mentioned sound while keeping her mouth open (gaping display) (Fig. 4). In the latter case, mating did not occur.

Discussion

Our study provides the first description of the breeding behaviour of *P. casuhatiensis*. It provides unprecedented information on the time of year when copulations occur, the environments in which they take place, and behavioural data that contribute both to the knowledge of its natural history and to the implementation of conservation measures. Although this is a rare species, the intensity of the study resulted in a significant number of records (12 encounters involving 13 individuals) and the fact that we conducted the study entirely in the field increases the representativeness and value of the results obtained. Even so, the number of observations remains small and limits the conclusions that can be drawn from them, particularly regarding the possible changes in behaviour in response to temperature reported.

The courtship and copulation activity of the Casuhatien anole occurs between October and November; and this result is consistent with published records for *P. achalensis*, a species endemic to the Sierras de Córdoba, Argentina [4, 48]. Knowledge of the months when individuals are reproductively active is of particular value, especially considering that reproductive behaviour makes the individuals more visible and vulnerable in areas subject to tourist activity [5], and with a history of illegal capture [6].

All the copulations we recorded happened in bare rock environments, where we also found the majority of solitary individuals of both sexes. Studies by Schwarzkopf and Shine [41], Shine [43] and Sullivan and Kwiatkowski [46] reported a trade-off between mating and predation risk in different groups of animals, particularly lizards. Males become more visible during courtship and their energetically costly displays may also reduce their eventual resistance to predation [42], reducing adult survival, and consequently, population abundance [29]. Although we did not observe predation events, we can reasonably assume an increased vulnerability during breeding, especially in light of some anthropogenic changes in the environment, such as the spread of exotic woody plants that provides perches for aerial predators, and may increase their abundance or hunting efficiency.

Fig. 4 Female Casuhatien anole (*Pristidactylus casuhatiensis*) showing rejection behaviour towards a male attempting to copulate in the Ventania system (Buenos Aires, Argentina)

Comparison of the reproductive behaviour is limited due to the scarcity of studies describing this aspect of saurian natural history, especially in natural environments. Regarding the total duration of copulation, Gasparotto et al. [15] describe mating under natural conditions in the Noronha skink (*Trachylepis atlantica*) endemic to Fernando de Noronha, Brazil, which also inhabits rocky surfaces, and report much shorter times (much less than half) than those that we recorded for *P. casuhatiensis*. Studies focusing on three arboreal or semi-arboreal leiosaurids of the genus *Enyalius*, one endemic to Brazil, and the other two with wider distributions, report times closer to the one we report [2, 19, 25]. All these studies account for intraspecific variations in the duration of courtship and copulation, which is also the case in our species. [3, 26] studied reproductive behaviour in species of the genus *Anolis* and argue that copulation length may be the result of environmental conditions or even an effect of disturbance caused by the presence of a nearby observer. Although we cannot completely rule out the latter for our study, we made efforts to minimise observer interference (minimal, slow movements and silence).

The sex ratio of the individuals involved in the reproductive encounters described (five males and eight females) agrees with the generally polygynous mating pattern of saurian [33]. This is also consistent with the territoriality of the males, especially during the breeding season, as reported by Naretto and Chiaraviglio [24] for *Pristidactylus achalensis* and reflected in our case by aggressive encounters and signs of biting on the head observed during the field work.

The behaviour of *P. casuhatiensis* during pair formation and subsequent mating is consistent with the general patterns described by Carpenter [8] for iguanids, including the proactive attitude of the courting male, the pursuit of the female, and the mode of attachment. Similarly, the actions associated with the different courtship phases are consistent with those of other squamate families such as Scincidae [34], Tropiduridae [31] Teiidae [37], and Liolaemidae [13].

The courtship sounds recorded in this work correspond to uniform emissions that do not result from the vibration of the vocal cords; rather, they are of guttural, produced by a violent exhalation of air [17, 38]. Labra et al. [17] and Laspiur et al. [18] mention that these sounds are often associated with aggressive postures and are emitted in response to threatening conditions, such as handling or exposure to different stimuli. Within the Leiosauridae family, [38] associate hissing sounds with antipredator behaviour, while Laspiur et al. [18] argue that those sounds occur during aggressive encounters and include warning and attack calls. We found no records describing the emission of sounds in a reproductive context associated with the rejection of a mating attempt by the female; however, this rejection behaviour occurs in females of *Tropidurus torquatus*, a species with a wide South American distribution. Silva et al. [44] suggest that there may be a tendency to select for larger males during the breeding season because they are dominant males and would defend well-defined territories. Young males occupying adjacent territories would find it difficult to access females and would only do so when dominant males are absent. In this regard, it is interesting to note that the situation recorded in our paper involved a young male and occurred in mid-December, when we no longer recorded mating in the study area.

Conclusions

In this work we determined that the reproductive activity of the Casuhatien anole is concentrated in the spring, particularly in the early afternoon, following the patterns described for other species of lizards. We also identified rocky outcrops above 600 m altitude as the habitats where courtship and copulation takes place, and described the mating behaviour. During these events individuals appear to be particularly vulnerable to humans and predators, and this should be taken into account when planning their conservation, especially with regard to the protection of reproductive habitats and the regulation of tourist activity.

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Authors' contributions
DLO and AA designed the study and carried out the field sampling. DLO and SMZ carried out the design, analysis and writing of the paper. All authors read and approved the final version of the manuscript.

Availability of data and materials
All data generated or analysed during this study are included in this published article.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable; this is a literature review of published sources

Competing interests
The authors declare that they have no competing interests.

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