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Phymaturus cf. *palluma* in captivity: observations on its reproduction and biology

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Abstract. The herbivorous high-altitude iguanid lizard *Phymaturus* cf. *palluma* is adapted to the climatic extremes of the Chilean High Andes. It has been thought of as impossible to keep long-term and propagate in captivity. If a number of key parameters, such as a substantial decrease in temperature at night, a wide temperature gradient during the course of the day, proper air exchange, high light intensity with UV-irradiation, and cold hibernation, are taken care of, the species can be kept in a terrarium for a period of at least twelve years, however. Reproduction under terrarium conditions was successful as well and is reported on here for the first time. Two females gave birth to one and three young, respectively. Data are provided on the number per litter and sizes of neonates, and courtship behaviour is detailed. A unique observation revealed similarities between its reproductive behaviour and that of *Uromastyx* and *Phrynosoma,* respectively, which have not been described before.

Key words. Squamata, Iguanidae, Liolaeminae, *Phymaturus palluma*, reproduction, biology, captivity, Chile, Argentina, South America.

Introduction

Phymaturus palluma is a moderately large, dorsoventrally compressed lizard with a spiky tail and a snout–vent length of up to 110 mm (Cei 1986, Donoso-Barros 1966, Hellmich 1934) (Fig. 1). It is native to the Alpine zone of the central Andes of Chile and Argentina (Cei 1986, Lobo & Quinteros 2005). The nomenclature of the species, whose type series was collected by Charles Darwin during his famous journey on the research ship "Beagle", was the subject of long controversy until a ruling by the ICZN fixed the internationally well-established name *Phymaturus palluma* (Molina, 1782) as the only valid denomination; a summary of the nomenclatural history of the species can be found in Werning (2009).

The lizard with its peculiar habitus is well known to the local population and referred to as "matuasto". Scientific research into *Phymaturus palluma* dates back to the 1920' and 30' when the German herpetologist Walter Hellmich focused on this species and was the first to try and keep it in a terrarium (Hellmich 1934, 1936). As his attempts were summarily unsuccessful, the lizard has been thought of being unsuited for the terrarium ever since, with the extreme ecological and dietary requirements of the species creating problems that seemed impossible to resolve (Schifter 1965, Kästle 1980, Obst et al. 1984, Bosch & Werning 1991, Schmidt & Henkel 1995).

Information on *Phymaturus palluma* used to be scant, comprising just thirty scientific publications and a mere three that dealt with its captive needs by the early 1990' (Eisenberg 1994). The state of knowledge of the taxonomy and phylogeny of the genus *Phymaturus* has been notably improved only during the past few years (e.g., Lobo & Quinteros 2005, Lobo et al. 2010). After *Phymaturus* was regarded as monotypic for a long time (e.g., Peters & Donoso Barros 1970), numerous new taxa have been differentiated since the 1980' and during the last ten years in particular, and today the genus comprises thirty-five nominal species (Lobo et al. 2010, Núñez et al. 2010, Uetz 2012).

Material and methods

A total of three males, two females and one juvenile were kept in terraria for longer periods of time during 1989–2001 (Tab. 1), the insights gained from which have been reported elsewhere (Bosch & Werning 1991, Eisenberg 2003). Several journeys to the natural habitats of *Phymaturus palluma* in Chile during the time from 2001 to 2004 afforded the junior author opportunities to collect and export several specimens, which saw a total of nine males and eleven females being imported into Europe. These specimens originated from Termas de Chillán, near Chillán, Región del Biobío, Chile, and were originally identified as *P. palluma*.

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Table 1. Age, measurements and weights of selected Alpine chuckwallas (*Phymaturus* cf. *palluma*) in the care of TE. (r) indicates a regenerated tail.

Spec. #	Period of keeping	SVL [mm]	TL [mm]	Minimum and maximum weights [g]	Annotations
1	1993–2003	94	97	22–37	Male (SMF 83674); green dorsal pattern; received adult in 1993; reached at least twelve years of age
2	1993	85	95	20	Male (SMF 77090); died of emaciation
3	1993	86	57 (r)	21	Female; died of emaciation
4	2001–today	85	103	27	Male; now Pair 2; yellow dorsal pattern
5	2001–today	98	61 (r)	31–38	Female; now Pair 1; gave birth in 2001 and 2005
6	2001–19.02.2012	86	88	22–29	Female; Pair 2; gave birth in 2004
7	2003–today	99	64 (r)	42–47	Male; now Pair 1; yellow dorsal pattern
8	2003–2004	83	90	24	Subadult female (SMF 83675); perished during hibernation
9	2003–2004	92	84	18	Subadult female (SMF 83676); perished during hibernation

In the wake of the numerous descriptions of more species in this genus, the distribution range of *P. palluma* was restricted to Argentina, however (Núñez et al. 2010). Núñez (pers. comm.) identifies our animals by photo and locality as possible *Phymaturus vociferator*, but states that the population of Termas de Chillán is not yet studied. Because we cannot therefore identify our individuals to species level in accordance with the new taxonomy of the genus on the one, but cannot rule out the existence of further cryptic species on the other hand, we have opted for referring to them as *Phymaturus* cf. *palluma* at this point of time.

The imported lizards were split up amongst various experienced lizard keepers and accommodated under different conditions. This demonstrated that a number of husbandry concepts were unsuited, as they caused the lizards to become unwell and some of them to perish. However, the experiments also yielded two approaches to husbandry management that appear fundamentally appropriate.

Today, we keep our *P.* cf. *palluma* in pairs in terraria of at least 50 × 50 × 70 cm (length × width × height) in dimension. The bottom substrate consists of moist river gravel or potting soil on which stacked flakes of sandstone, pieces of roots and bark create a network of shelters. In some instances, the rear and side walls consist of imitation rock faces that offer plateaus and crevices.

TE uses outdoor terraria that are run without any artificial lighting from March through November. For their part, indoor terraria are illuminated and heated with iodine vapour lamps (HQI, 70 W) and spotlights with an emission of UV-light (e.g., 100 W "Active UV Heat") in emulation of the annual cycle as per Tab. 2. Outfitted thus, day temperatures of 20–25°C are created in the indoor terraria while the outdoor tanks are subject to ambient values. Temperatures at night decrease by a minimum of 10°C at the location where they are set up.

Figure 1. A male *Phymaturus* cf. *palluma* with a green dorsal pattern in a terrarium. Photo by T. Eisenberg.

Table 2. Management of the photoperiod applied in the captive husbandry of Alpine chuckwallas in the care of TE, emulating conditions in their natural habitat at Coquimbo (30° S, 72° W), Chile.

Month [in accordance with adjustment to a northern hemisphere cycle]	Corresponding to month in natural habitat	Hours of artificial daylight
January	July	none (hibernating)
February	August	11
March	September	12
April	October	13 or kept in outdoor terrarium
May	November	14 or kept in outdoor terrarium
June	December	14.5 or kept in outdoor terrarium
July	January	14.5 or kept in outdoor terrarium
August	February	13.5 or kept in outdoor terrarium
September	March	12.5 or kept in outdoor terrarium
October	April	11.5
November	May	none (hibernating)
December	June	none (hibernating)

Each terrarium sports a bowl with fresh water, and the lizards are fed daily with a range of leafy lettuces such as rucola (arugula), field, Roman, endive or common lettuce, herbs like basil, parsley, mint and thyme, and grated carrots, added to which are wild herbs such as the leaves and flowers of dandelion, ribwort, comfrey, stinging nettle, clover, and the leaves of wild strawberries during the summer months. The outdoor terraria hold planting trays with the mentioned wild herbs to ensure a constant fresh supply to which the lizards can help themselves. All food offered is fortified with the vitamin/mineral supplement "Korvimin Ziervogel plus Reptil™" (WDT, Garbsen, Germany) at regular intervals. Food of animal origin is accepted only occasionally, and only by certain individuals. An exception is the caterpillars of the waxmoth.

SMF refers to the herpetological collection of the Senckenberg Museum, Frankfurt/M., Germany.

Results and discussion

Husbandry conditions

More detailed knowledge of the natural habitat of *Phymaturus* cf. *palluma* together with realisations gained from subsequent husbandry experiments under different conditions have demonstrated that the following aspects are key to the successful long-term captive keeping of this lizard: (1) distinctly decreased temperatures at night; (2) presence of a distinct temperature gradient in the terrarium during the day with relatively low air temperatures, but high values in spots that are protected from wind; an air temperature of at least 20°C appears to be necessary to trigger activity in these lizards; (3) perfect ventilation of the terrarium; (4) high intensity of light that contains UV-radiation; (5) a distinct seasonal rhythm including hibernation at low temperatures.

Our evaluation of basic requirements was supported by the problems and losses we experienced amongst the specimens imported in 2001. These insights then led to the formulation of the following husbandry management strategies:

TE keeps his specimens in pairs according to the seasonal rhythm of the Northern Hemisphere. This entails that the lizards are slowly woken from hibernation in March by temporarily housing them in a terrarium set up in an unheated garage before they are released into their outdoor tanks (Fig. 2). Hidden in their artificial rock crevices, they tolerate minor frost at night without any problem here. Depending on general weather patterns, they may stay in their outdoor terraria until the first nightly frosts in November. Following another transition period of four to eight weeks in a tank in the garage, like in spring, the lizards are then overwintered at 4–8°C in a refrigerator.

HW keeps his specimens in an otherwise uninhabited room in back premises. This structural situation provides a greatly buffered temperature range throughout the year with the room remaining relatively cool even at high outside temperatures. The lizards are subjected to the seasonal rhythm of the southern hemisphere. "Their" summer thus falls into the Central European winter, when the terrarium is illuminated for about 15 hours every day and the room is heated to an air temperature of about 22°C by means of a central heating system. Heating is then switched off in the evening and the windows are left slightly ajar. The windows are closed during periods of severe frost so that cooling at night is driven indirectly by low outside temperatures and no heating. This results in night temperatures of 4–12°C. Spring and early summer weather at our latitude is then used to emulate autumn for the lizards. The windows are left open all the time, and the room is not heated, so that room temperatures fluctuate in dependence on the outside conditions within a range of 15–22°C during the day. At night, values decrease to near outside temperatures, usually to 8–18°C. At the same time, the daily period of illumination is gradually reduced to about eight hours of daylight and switched off completely for about two weeks during a phase of cooler weather. High summer then sees the lizards hibernating in a refrigerator (see below). Spring is subsequently emulated for them during the Central European autumn when the Alpine chuckwallas are returned to their terraria and kept as they would during their autumn phase, only along an inverted timeline. The difference here is that temperature levels are raised more rapidly by switching on the central heating. The lizards enter winter with an empty digestive tract after they will usually have spontaneously ceased feeding when temperatures decreased and the hours of artificial daylight were shortened (from about mid-October in nature).

The captive husbandry of *Phymaturus palluma* has always been regarded as being difficult to the extreme (Hellmich 1936, Schifter 1965, Bosch & Werning 1991, Schmidt & Henkel 1995). Even after our experiences of the past years, the species continues to be highly problematic and technically demanding. Our preliminary data and results confirm a life expectancy of at least twelve years for this species. Aside from emulating distinct diel and seasonal climatic fluctuations, transporting them as rapidly and considerately as possible and so limiting the loss of body fluids and energy to the minimum is pivotal to their successful adaptation to terrarium conditions. As far as their husbandry in a terrarium is concerned, distinctly decreased night temperatures are of utmost importance, as data from the natural habitats of these lizards show that nightly values routinely drop to near or below freezing point. On the other hand, day temperatures of 20–25°C with localised hotspots offering more than 35°C need to be reached for the lizards to become fully active. These daily values are also of critical importance for the proper functioning of their digestive processes.

No other group of lizards has produced herbivory as often as the subfamily Liolaeminae during its course of evolution (presumably 18 times independently; Espinoza et al. 2004). In contrast to what has so-far been most commonly accepted as preconditions for the evolution of herbivorous squamate reptiles, the representatives of the subfamily Liolaeminae stand out by their small adult sizes and being adapted to comparatively cold climates (Espinoza et al. 2004). Considering that a vegetarian diet necessitates high body temperatures to keep the required bacterial and protozoan symbionts in the digestive tract functional, a small body size offers advantages with regard to thermoregulation within a cold environment. The natural habitats of Alpine chuckwallas are marked by highly changeable and windy weather with irregular periods of sunshine during which the sunlight heats up individual spots on rocks. These sources of warmth are exploited by the Alpine chuckwalla particularly efficiently not only by its having a dorsoventrally compressed build, but also by a principally dark dorsal colour pattern and, in the case of *P.* cf. *palluma,* a dark pigmentation of the peritoneum (T. Eisenberg unpubl. data). With their preferred body temperature of more than 30°C, the herbivorous representatives of the Liolaeminae do not differ from other herbivorous lizards (Espinoza et al. 2004).

Keeping Alpine chuckwallas during their active period in an outdoor terrarium during the Central European summer appears to be principally possible after adjusting them from the Chilean (southern) annual cycle to ours (own observations, K. Busse pers. comm.). Exposure to outside conditions furthermore had visibly positive effects on the intensity of their colours and activity. After having become outright tame from spending time in a terrarium, the lizards rapidly returned to exhibiting a natural shyness in their outdoor tanks, responding once more, for example, with sheltering to the moving shadow cast by a passing bird.

Figure 2. Two outdoor terraria for keeping *Phymaturus* cf. *palluma*. Photo by T. Eisenberg.

Reproduction and ontogenetic development

A neonate born from a female shortly before her death on 21. March 1993 in the care of TE still had a yolk sac of about 3 cm^3 in volume attached and died from suffocation in its amniotic membrane (SMF 81867). Measurements and weights of all neonate *Phymaturus* cf. *palluma* born in the care of the authors are summarised in Tab. 3.

Of the specimens imported in late February of 2001, two females subsequently also gave birth to young (Werning 2004, T. Eisenberg unpubl), with four being born after being in the care of HW for three weeks, and another four five weeks after having entered the collection of TE.

During the entire observation period, TE witnessed mating events in June of 2002 and again after hibernation in March of 2003 and 2011 (Fig. 3), whereas HW recorded a corresponding observation once in October of 2004. The copulation events witnessed by TE played out with the pair hanging vertically on the imitation rock rear wall. In the case of the mating observed by HW, the male was found sitting in front of the female that was lying on her back, trying to grab her by the neck with his mouth in order

Table 3. Measurements and weights of newborn juveniles of *Phymaturus* cf. *palluma*.

Juvenile #	Date of birth	SVL [mm]	TL [mm]	Weight [g]	Breeder	Annotations
1	21.03.1993	40	32	n/a	TE	SMF 81867; large yolk sac, not viable
2	20.03.2001	40	41	3.5	HW	
3	20.03.2001	43	44	3.5	HW	
4	20.03.2001	38	40	4.0	HW	
5	20.03.2001	42	44	4.0	HW	
6	06.04.2001	40	41	4.0	TE	
7	06.04.2001	44	43	3.0	TE	SMF 83678; perished on 28.06.2001
8	06.04.2001	38	40	3.5	TE	SMF 83677; with remains of umbilical cord; perished on 18.08.2001
9	06.04.2001	46	40	3.5	TE	
10	14.04.2003	45	43	6.0	van den Heuvel	SMF 82557; female died of birthing complications; juvenile dead
11	09.12.2004	46	40	4.0	TE	with remains of umbilical cord
12	09.12.2004	45	40	4.0	TE	
13	09.12.2004	40	41	4.0	TE	with remains of yolk sac
14	presumably 29.01.2005	46	42	4.0	TE	not in a terrarium

to turn her around. Failing to achieve this, he eventually started dragging her through the terrarium while she was still on her back. The female then suddenly righted itself and tried to run away. The male pursued her, managed to place a holding bite on her neck, and initiated copulation. The latter took about five minutes. White deposits were noted on the back of the females after all witnessed mating events.

In the collection of TE, female #6 (Tab. 1) presented herself as particularly voracious from early October 2004 and rapidly gained in body volume (Fig. 4). She was furthermore notable for selecting a hiding place under a piece of bark that was within the range of a spotlight. All this hinted at a possible instance of gravidity. This female stopped leaving her shelter spot altogether from the beginning of November and ceased feeding while her girth continued to increase. The birthing process then commenced with the appearance of the first young on 9. December 2004 around 12.00 h, followed by another two siblings at intervals of some 15 minutes (Fig. 5 A, B). None of the newborns were enveloped in intact membranes, as had been the case in the 1993 birth mentioned above. Two neonates still had remains of the umbilical cord attached, and one was noted for having a lentil-sized yolk sac, though. All births were preceded by heavy contractions visible in the female's belly region while she had positioned her hind legs at a slight angle, whereas the actual extrusion of a baby only took a few seconds. All neonates appeared very lively right after birth (Fig. 5 C). They were collected from the terrarium and housed separately on a substrate of moist cellulose after the remains of the umbilical cords had fallen off and the navel had been treated with iodine. A few hours later, they

Figure 3. Mating in *Phymaturus* cf. *palluma* in a terrarium. Photo by T. Eisenberg.

Figure 4. A female *Phymaturus* cf. *palluma* with a body cavity tautly filled with three embryos towards the end of the gestation period. Photo by T. Eisenberg.

were transferred to a nursery terrarium. Measurements and weights of these juveniles are summarised in Table 3.

As for her part, the female weighed a mere 22 g after having given birth and showed heavily sunken flanks. She was very lively, however, and seen feeding and drinking for the first time the next day. The male, which had hardly shown himself over the past few days, reappeared immediately after the births and tried to court the female by assuming a bright light yellow colouration, but was kept at bay by the female biting after it.

Female #5 was likewise hardly ever seen in December of 2004 and January of 2005. On 29. January 2005, a newly born juvenile was discovered. It was impossible to forensically reconstruct whether this litter originally comprised more neonates.

The juveniles born in 2001 were housed in terraria that were outfitted and decorated like those for the adults. They preferably sheltered in the cavities of unfired hollow bricks where humidity levels were constantly elevated, and readily commenced feeding on plant matter after they had lived off the remains of their yolk sacs for the first three days (Fig. 6). The juveniles proved sensitive to particularly high temperatures in summer and were for the first time overwintered for two months together with the adults in a refrigerator at an age of seven months. The young born in 2004/2005 moulted for the first time at an age of two and a half months. Compared to adult specimens, the tail length of juveniles is marginally shorter than the snout–vent length (Tables 1, 4, 5). Data on their average growth and weights are given in Tables 4 and 5. The sexes of the juveniles could be identified when they had reached an age of fourteen months on the basis of male specimens exhibiting up to twelve conspicuous preanal pores.

Births from imported gravid females were so far exclusive to the period February through April, corresponding to late summer in this lizard's country of origin. That these dates of birth contradict the findings of Habit & Ortiz

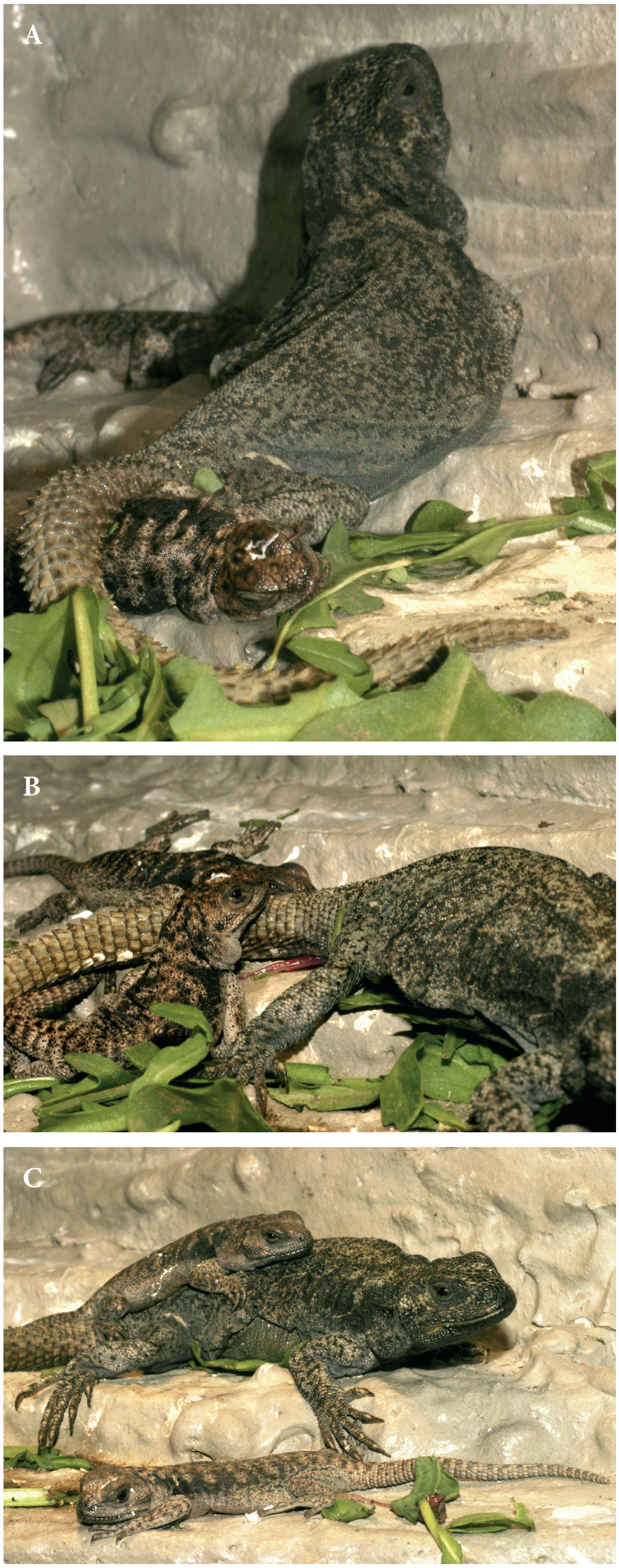

Figure 5. Birthing event in *Phymaturus* cf. *palluma*: (A) Extrusion phase of birth; (B) newly born juvenile with remains of the umbilical cord; (C) mother specimen with two freshly despatched neonates. Photo by T. Eisenberg.

Figure 6. Juveniles of *Phymaturus* cf. *palluma* feeding on a dandelion flower. Photo by T. Eisenberg.

Table 4. Average growth in juvenile Alpine chuckwallas in the care of HW during 2001 (mean ± standard deviation [n = 4]).

Weighed on day of life	1.	60.	90.	120.	150.	180.	240.	365.
SVL [mm]	40.8 ± 2.2	53.0 ± 2.4	62.0 ± 4.7	60.5 ± 4.2	62.0 ± 4.8	62.5 ± 5.0	62.0 ± 3.6	71.8 ± 8.0
TL [mm]	42.3 ± 2.1	52.8 ± 3.8	59.8 ± 6.1	58.0 ± 7.7	61.0 ± 6.7	62.5 ± 5.0	63.0 ± 7.7	70.8 ± 12.2
weight [g]	3.75 ± 0.3	7.0 ± 0.8	7.5 ± 1.0	8.0 ± 1.6	8.0 ± 1.6	9.3 ± 2.2	9.0 ± 2.0	15.0 ± 3.5

Table 5. Average growth in juvenile Alpine chuckwallas in the care of TE during 2001 and 2004 (mean ± standard deviation); M = male, F = female.

Juveniles in 2001	Weighed on	06.04.2001	28.06.2001	15.08.2001	28.10.2001	09.06.2002	
	Number of specimens	n = 4	n = 1	n = 3	n = 2	n = 2	
						M	F
	SVL [mm]	42 ± 3.7	47 ± 0	49.7 ± 2.5	54 ± 1.4	72	65
	TL [mm]	41 ± 1.4	42 ± 0	48.3 ± 2.9	52.5 ± 3.5	72	65
	weight [g]	3.5 ± 0.4	n/a	n/a	7.0 ± 1.4	15	12
Juveniles in 2004	Weighed on	09.12.2004	09.01.2005	09.02.2005	23.04.2005	10.07.2005	
	Number of specimens	n = 3	n = 3	n = 3	n = 3	n = 3	
	SVL [mm]	43.7 ± 3.2	46.0 ± 1.7	47.3 ± 2.5	52.7 ± 0.6	64.0 ± 1.0	
	TL [mm]	40.3 ± 0.6	43.7 ± 1.5	47.0 ± 4.4	48.3 ± 0.6	60.7 ± 4.0	
	weight [g]	4.0 ± 0	4.5 ± 0.9	4.8 ± 1.0	5.8 ± 0.3	9.7 ± 0.6	

(1996) could be based on macro- and/or microclimatic circumstances (population-specific differences) and/or temporal factors (Habit & Ortiz based their results on observations made during a single year with nothing being known about this specific year's weather conditions), and/or even influences arising from the conditions their specimens were exposed to during transport. Some of our Alpine chuckwallas were transported for nearly three weeks before they eventually arrived in our terraria. During this period they were unable to actively thermoregulate, which could have temporarily slowed embryonic development. On the other hand, mating events in specimens that were overwintered here were recorded right after hibernation (in contrast to the findings by Habit & Ortiz l.c.) as well as in summer. In the wild, the gestation period of *P.* cf. *palluma* would extend over two activity periods separated by a hibernation interval and span some twelve months (Habit & Ortiz 1996). Young would then be born three to two months prior to the next hibernation interval. Be that as it may, the mean ground temperature is too low for the incubation of eggs, at least in parts of the distribution range, for which reason Alpine chuckwallas – like some syntopic species of *Liolaemus* – have resorted to a vivioviparous reproductive strategy. The births in our winter (December 2004 and January 2005) might be a consequence of our not having adhered to timely overwintering the respective females so that the embryos were not forced to insert the diapause that is obligatory in nature. It demonstrated, however, that a shortened gestation period as a result of omitting such a period of dormancy has no negative effects on the embryonic development. An argument supporting that the switch-over to the annual cycle of the Northern Hemisphere of our wild-caught specimens might not yet have been completed at the time is provided by the fact that mating events were witnessed right after the first hibernation period, whereas Habit & Ortiz (1996) noted these only in high summer in the wild.

Some of the described observations show certain analogies to the Old World genus *Uromastyx* from which the presence of "markings" in the shape of urate deposits on the dorsum of mated females is also known (T. Wilms, pers. comm.), as is the evasive response to mating attempts by unreceptive females turning on their back (Wilms 2001). Baur & Montanucci (1998) documented a copulation event with the female being in a dorsal position in *Phrynosoma coronatum.*

As far as the number of neonates in a litter is concerned, *P. palluma* is known to give birth to between three and five young (Cei 1986). The birthing events in 2001 and 2004 showed that the involved females of our *P.* cf. *palluma* were at their maximum physical carrying capacity with three foetuses in two, and four in one instance, respectively. The total mass of newborns, excluding amniotic fluids and membranes, corresponded to 35 and 45% of the maternal weight, respectively. Owing to the facts that sizes and weights of juveniles born so far in our care were very similar (Tab. 3), and the weight of female #6 after birth already fell within the range of a cachexic specimen (Tab. 1), it is difficult to believe that a litter could possibly comprise more than four neonates. Our data thus contradict Cabezas Cartes et al. (2010) who stated that this species would only produce one or two juveniles per litter. It is as yet unknown as to which extent the birth of only one baby could be a consequence of husbandry conditions or whether instances like that routinely occur in nature at all. Habit & Ortiz (1996) regarded the exceptionally large size of neonates as a determinant of the reproductive cycle of this species: With the females being filled to capacity with embryos towards the end of the gestation period, their stomachs and digestive tracts would be strongly compressed, rendering the processing of food nearly impossible. It would therefore prevent females from building up reserves for hibernation during this period. Accordingly, they need the remaining two to three months after birth to physically recover sufficiently and stand a chance of surviving hibernation.

Social behaviour

The intermittent shows of a distinctly aggressive behaviour by the male caused us to remove newborns from the terrarium of their parents right after their birth to ensure their safety, even though Halloy & Halloy (1997) reported on expressions of maternal care in various Andine representatives of the genera *Liolaemus* and *Phymaturus*.

Alpine chuckwallas exhibit a territorial behaviour that appears to be dependent on the structure of the individual surroundings (observations made by HW; Habit & Ortiz 1994): In areas with small, individual rocks, the lizards would typically live in pairs, and the home ranges of both sexes would overlap widely. In situations where there are large boulders with numerous crevices, i.e., shelters, *Phymaturus* cf. *palluma* would establish and maintain a strict social hierarchy, however. Here, the home ranges of males do not overlap and several females will live within their boundaries.

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