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Developmental aspects of the Crau Plain Grasshopper, *Prionotropis hystrix* (Germar, 1817) ssp. *rhodanica* Uvarov, 1923 (Orthoptera: Pamphagidae), over one generation in captivity

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Abstract

Eight egg-pods of *Prionotropis hystrix* ssp. *rhodanica*, layed in June 2022 ex-situ by females from the Crau, were provided for rearing by the project LIFE SOS Criquet de Crau, Saint-Martin-de-Crau, France. Both egg-pods and single eggs were hibernated (with 80% of embryonic development) in the lab (Jena, Germany) from October 2022 until March 2023, and after that put in warm environment for hatching. The eggs showed a considerable resistance against drought with few mass and water loss. Hatching started after 3-4 weeks (at Ø 19°C), but hatching success amounted to only 22% for all intact eggs. Despite warm conditions (and water supply), several eggs stagnated in their embryonic development at late katatrepsis. Because of high first instar mortality only one juvenile survived, moulted over five instars, each of 12 days (21-26°C) to an adult female, which lived for further three months, with egg-laying every two to three weeks (~27°C).

Keywords: diapause, eggs, egg-pods, embryonic development, food, hatching

Zusammenfassung

Entwicklungsaspekte der Crauschrecke, *Prionotropis hystrix* (Germar, 1817) ssp. *rhodanica* Uvarov, 1923 (Orthoptera: Pamphagidae), über eine Generation in Gefangenschaft. Acht Ootheken von *Prionotropis hystrix* ssp. *rhodanica*, abgelegt im Juni 2022 ex-situ von Weibchen aus der Crau, wurden vom französischen Projekt LIFE SOS Criquet de Crau, Saint-Martin-de-Crau, zur Verfügung gestellt. Sowohl Ootheken als auch einzelne Eier wurden (bei 80% Embryonalentwicklung) in einem Labor in Jena/Deutschland von Oktober 2022 bis März 2023 überwintert und danach für den Schlupf in Wärme gestellt. Die Eier waren sehr trockenheitsresistent mit geringem Masse- bzw. Wasserverlust. Der Schlupf setzte nach 3-4 Wochen (bei Ø 19°C) ein, doch der Schlupferfolg betrug nur 22% für alle intakten Eier. Trotz Wärme (und Wasserverfügbarkeit) stagnierten etliche Eier in ihrer Embryonalentwicklung in der späten Katatrepsis. Aufgrund hoher Sterblichkeit der Erstlarven überlebte nur ein Tier, das sich über fünf Stadien, jedes von etwa 12 Tagen Dauer (21-26°C), zum adulten Weibchen entwickelte. Dieses überlebte weitere drei Monate, mit Eiablagen alle zwei bis drei Wochen (~27°C).

Schlüsselwörter: Diapause, Eier, Embryonalentwicklung, Nahrung, Ootheken, Schlupf

Introduction

The Crau Plain grasshopper is an endemic species in the Crau of Southern France, listed both in the French national Red List (Sardet & Defaut 2004) and in the IUCN Red List as CR (critically endangered) (Foucart & Lecoq 1998, Hochkirch et al. 2016). Their habitat is the extremely dry steppe of the Crau, which has been considerably reduced and fragmented in recent decades by irrigation-based agriculture, horticulture (peaches, apricots), roads, industrial and military complexes. This, combined with a strong philopatry and low population density, has led to a decline in the Crau grasshopper over the last two decades, even in protected areas (Foucart & Lecoq 1998, Hochkirch et al. 2014, Hochkirch 2017).

According to the conservation strategy (Hochkirch et al. 2014) and following conservation studies (by the Hochkirch group), the actual project LIFE SOS Criquet de Crau (2021-2025) was launched to coordinate and study the main aspects of its protection, including its life cycle. Meanwhile, several studies in the field and in the laboratories were carried out, e.g. referring to population genetics (Piry et al. 2018), habitat structures and microhabitat preferences (Bröder et al. 2018), and estimation of population sizes (Bröder et al. 2019). While juvenile and adult development is well known, including in wild populations (summarized by Defaut & Morichon 2015), the situation for egg development is still incompletely understood. Therefore, the few results of an ephemeral laboratory study (at the University of Jena, Germany) covering the entire developmental cycle from egg-pod to egg-pod, with a focus on egg development, based on the final CPG-report Jena (G. Köhler, 2022-2023), may be of some interest.

Material and Methods

Egg-pod origin

Eight egg-pods of *Prionotropis*, four each from Corréze and La Barben, were layed in these ex-situ stations in June 2022, and transferred immediately after laying to the wild in the Calissane area of the Crau. There they were dug in the upper soil layer, labelled, and left for four months until October. Then they were dug out and sent on 25.10.2022 to the Institute of Ecology and Evolution of the Friedrich Schiller

University of Jena (Thuringia, Germany) (Table 1) for further developmental studies. The filter paper around the individual egg-pods was lightly moistened every three days, before the egg-pods were treated beginning on 03.11.2022.

Table 1: Origin of *Prionotropis* egg-pods (all dates 2022). Compilation by L. Zechner.

Nb.	Ex-situ station	Egg laying	Transfer to Crau	Dispatch Jena
80	Corréze	19.-25.06.	28.06.	25.10.
84	Corrèze	19.-25.06.	28.06.	25.10.
124	Corrèze	19.-25.06.	28.06.	25.10.
127	La Barben	-06.06.	07.06.	25.10.
143	La Barben	-06.06.	07.06.	25.10.
172	Corrèze	12.06.	16.06.	25.10.
186	La Barben	20.06.	21.06.	25.10.
190	La Barben	20.06.	21.06.	25.10.

Egg-pod treatment

From the eight egg-pods, seven were measured with an electronic caliper, and one egg-pod (nb. 143, which was broken) was opened to count the eggs and to treat them separately (see egg treatment below). After measuring, each egg-pod was placed in a cup with a fine-grained soil/sand-mixture (Fig. 1), which was moistened and put in a refrigerator with temperatures of 4-7°C and a relative humidity of around 80% (Table 2).

Subsequently, from 14.11.22, four egg-pods were regularly moistened, and three egg-pods remained dry for more than four months until 27.03.23 (Table 2). At this date, the seven cups were brought into small cages (16 × 16 × 22 cm, each cage with one cup) on a lab window in warm conditions, and all cups were regularly moistened for further development. The temperature was continually (every 30 min) measured with a thermo-logger (Fig. 2), and air humidity varied around 60-70%. Finally, only nymphs from one egg-pod (nb. 80) hatched. On 08.05.23 all egg-pods were opened and the remaining eggs dissected for embryonic status.

Fig. 1: Cups with egg-pods of *Prionotropis*, prepared for hibernation, 03.11.2022. Photo: Günter Köhler.

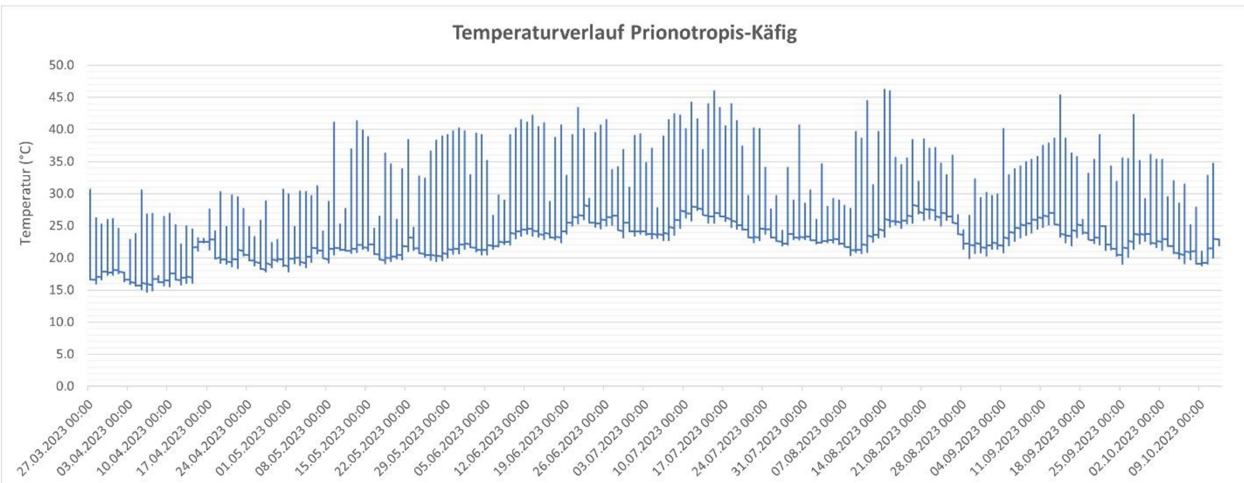

Fig. 2: Temperature curve (March-October 2023) over post-diapause, juvenile and adult development of *Prionotropis* in captivity. Graphic: Clemens Schulze.

Table 2: Treatment of *Prionotropis* egg-pods. L – length, Ø – diameter. +water / dry = soil/sand-mixture ± moistened resp. dry.

CPG No.	Origin	03.11.22		14.11.22	29.11.22	03.01.23	27.03.23
		L×Ø (mm)	fridge	fridge	fridge	fridge	lab/warm
80	Corrèze	19.4×11.4	+water	+water	+water	+water	+water
84	Corrèze	19.9×11.9	+water	+water	+water	+water	+water
124	Corrèze	15.6×13.3	+water	+water	+water	+water	+water
127	La Barben	16.9×12.0	+water	+water	+water	+water	+water
143	La Barben	broken → see Table 4a, b egg treatment					
172	Corrèze	16.6×12.7	+water	dry	dry	dry	+water
186	La Barben	14.4×12.2	+water	dry	dry	dry	+water
190	La Barben	17.9×12.4	+water	dry	dry	dry	+water
Defaut & Morichon (2015)		22.0×12.0					

Egg treatment

On 03.11.22 the broken egg-pod (no. 143) was dissected, containing a total of 17 eggs: 12 intact and 5 dried eggs. From these intact eggs two were opened (1 infertile, 1 with embryo ~80% developed, Fig. 3a). The remaining 10 eggs were carefully cleaned, and arranged in three rows (of each 4 resp. 2 eggs; resulting in egg number 1-10) on dry fine sand within an open small petri dish (Fig. 3b). This dish was placed in a larger petri dish with moistened filter paper and closed with a top, so creating a 100% relative humidity. Beginning on 29.11., only a dry filter paper was used, creating ~80% relative humidity (measured with a hygrometer in the fridge) for the following months. Already on 03.11.22 (before this procedure) the eggs were (1) measured under a stereomicroscope with an ocular micrometer (12,5 × 0,63 enlargement, 1 interval = 0.118 mm), and (2) weighted with a balance of Mettler Toledo XS105 DualRange (d = 0.01 mg) (see Table 4a, b). Afterwards, the eggs, together with the egg-pods, were put in the refrigerator with 4-7°C, and the egg mass was measured every two to three weeks (see Table 4a, b). At the end of March, after about five months of cooling (diapause), the eggs were taken from the refrigerator. In warmth, the sand with eggs in the petri dish was moistened, so that the eggs were provided with contact water. Now the eggs were weighted every 1-2 weeks and observed until hatch or final dissection at 08.05.23 (Table 4b).

Fig. 3: a) Embryo (~80% developed) of *Prionotropis* before hibernation, 03.11.2022; b) single eggs (egg-pod nb. 143) of *Prionotropis* on a soil/sand-mixture, 05.11.2022; c) two cages with egg-pods of *Prionotropis* in soil/sand-cups and herbs, prepared for hatching, 05.04.2023. Photos: Günter Köhler.

Juvenile and adult treatment

Beginning on 05.04.23, the cages were provided every 2-3 days with a mixture of fresh herb leaves (*Crepis, Ocimum, Rubus, Taraxacum, Thymus, Trifolium, Valerianella*) and grasses (*Festuca, Dactylis*) sampled around the Institute. The leaves were placed on the bottom of the cages, together with some moist filter paper (Fig. 3c). After hatch on 18./19.04.2023, six first instar nymphs died immediately, which were later measured (see Table 5). Only one nymph survived, which was provided mainly with the preferred *Plantago lanceolata* and *Taraxacum officinale*. After each moult, the exuvia was sampled and later measured to separate the juvenile stages (see Table 5). Few dried faeces of N5 and the young adult female were also measured.

Results

Egg-pod parameters

The length of the seven cleaned egg-pods varied considerably from 14.4 mm to 19.9 mm; their diameter ranged from 11.4 mm to 13.3 mm (Table 2). The egg-pods, treated in the above described way until end of march (~ 5 month of cooling), were then put in warm environment (Ø 20-27°C, see Table 5) until hatching and final dissection. In a total of 98 eggs were found in the seven egg-pods, with egg numbers varying from 10 to 17 per pod (Fig. 4), while one egg-pod (no. 190) was empty without any eggs (Table 3). Only 36 eggs (37%) were found to be intact (hatched or with embryo), whereas the remaining eggs were more or less dried, fungal or dented due to water loss. Therefore, the percentage of infertile eggs could not be calculated. Moistened treatment during hibernation resulted finally in considerably more intact eggs than in dry treatment, but in both treatments intact as well as damaged eggs occurred.

Fig. 4: Opened egg-pod (nb. 127), not hatched until May because of overall infertility, 08.05.2023. Photo: Günter Köhler.

Table 3: Final control of *Prionotropis* egg-pods, 08.05.2023.

Egg-pod no.	Content	Condition of eggs	Embryonic development
80 (moist)	10 eggs	all intact	3 infertile, 7 hatched
84 (moist)	14 eggs	all dried / fungal	3 infertile, 1 (80%), 3 (90%), remaining indefinable
124 (moist)	16 eggs	5 intact, 11 ± dried / fungal	2 infertile, 5 fungal, 3 (70%), 4 (80%)
127 (moist)	15 eggs	6 intact, 9 dented	all 15 infertile
143 separated	17 eggs	12 intact, 5 dried / fungal	1 infertile, 3 (≥ 70%), 3 (80%), 4 before hatch, 1 hatched
172 (dry)	14 eggs	indefinable	2 infertile, remaining ± den-ted
186 (dry)	12 eggs	3 intact, 9 ± dried / fungal	1 (>70%), 1 (<80%), 1 (90%)
190 (dry)	empty	no eggs	---

Egg parameters

Egg mass and water budget. The mass of 10 eggs (from one egg-pod) at the beginning of the diapause was rather constant, varying only from 30.1-34.0 mg (median 33.1 mg), with egg lengths of 9.2-9.9 mm (median 9.8 mm) and egg diameters of 2.1-2.3 mm (Table 4a).

The 10 eggs held for diapausing from 03.11.2022 until 27.03.2023 under low temperatures (4-7°C) and first 100% r. h., later 80% r. h. (always without contact of water) over these nearly five months showed little water losses, with only 3.7% on average. After transferred into the warmth and with contact water for further embryonic development, the water gain within two weeks increased by 22% on average, obviously independent on the embryonal development (Table 4a, b, Fig. 5).

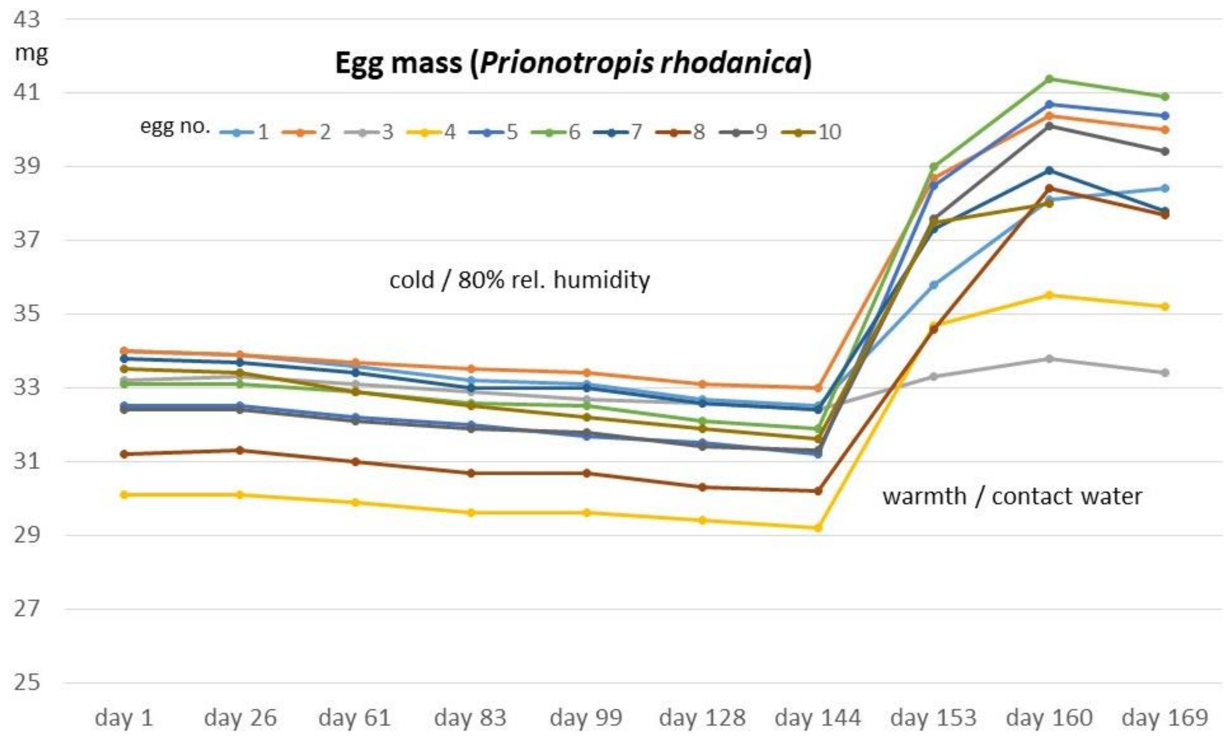

Fig. 5: Mass (mg) curves of single eggs over 170 days (Nov-April) under dry or wet conditions. Graphic: Günter Köhler.

Embryonal development. At the end of hibernation, the embryos were found in the same developmental stage (around 80%) like before. Only one egg (nb. 10) hatched after three weeks in warmth (Ø 19°C) on 21.04.2023, whereas the other nine eggs did not hatch until May. Therefore, on 08.05.2023 all remaining eggs were dissected, showing further four eggs immediately before hatch and five eggs still in embryo stages of 70-90% (Table 4b). Both in egg-pods and in single eggs it was striking that after five months of hibernation in 25 eggs the embryos were still developed until 70-90%, amounting to one third of all intact eggs (Table 3 and 4b).

Table 4a: Treatment of single *Prionotropis* eggs (egg-pod nb. 143) in a fridge under 4-7°C and 100%/80% relative humidity without direct contact of water. L – egg length, Ø – egg diameter, r. h – relative humidity.

Egg nb.	03.11.22 (→ 100% r. h.)			29.11.	03.01.23	25.01.	10.02.
	L (mm)	Ø (mm)	mass (mg)	→ 80% r. h.			
1	9.8	2.3	34.0	33.9	33.6	33.2	33.1
2	9.8	2.2	34.0	33.9	33.7	33.5	33.4
3	9.7	2.2	33.2	33.3	33.1	32.9	32.7
4	9.2	2.1	30.1	30.1	29.9	29.6	29.6
5	9.8	2.2	32.5	32.5	32.2	32.0	31.7
6	9.9	2.2	33.1	33.1	32.9	32.6	32.5
7	9.4	2.3	33.8	33.7	33.4	33.0	33.0
8	9.8	2.2	31.2	31.3	31.0	30.7	30.7
9	9.9	2.2	32.4	32.4	32.1	31.9	31.8
10	9.8	2.3	33.5	33.4	32.9	32.5	32.2
Min-max	9.2-9.9	2.1-2.3	30.1-34.0				

Table 4b: Continuation of Table 4a. *egg bursted.

Egg nb.	11.03.	27.03.	05.04.	12.04.	21.04.	08.05.23 / Embryo
	80% r. h.	→ contact water				
1	32.7	32.5	35.8	38.1	38.4*	dead, before hatch (♂)
2	33.1	33.0	38.7	40.4	40.0*	70-75%
3	32.6	32.4	33.3	33.8	33.4	80%
4	29.4	29.2	34.7	35.5	35.2	before hatch (♀)
5	31.5	31.2	38.5	40.7	40.4	70-75%
6	32.1	31.9	39.0	41.4	40.9*	80%
7	32.6	32.4	37.3	38.9*	37.8*	70-75%
8	30.3	30.2	34.6	38.4	37.7	>90%, shortly before hatch
9	31.4	31.3	37.6	40.1	39.4	before hatch (♀)
10	31.9	31.6	37.5	38.0	hatch	hatched, but dead in exuvia

Hatching and juvenile development

Hatching success. From the single 10 eggs of egg-pod nb. 143 only one egg (no. 10) hatched, bud died during moulting (Table 4b). From the remaining seven egg-pods only from egg-pod nb. 80 a total of seven eggs hatched. Taken the 36 eggs as intact, this accounted of a hatching success of 22%.

Juvenile development. On 12.04.2023, immediately after moistening the sand around midday, hatch emerged from egg-pod no. 80, resulting in seven first instar nymphs and their dry white exuviae of the vermiform nymph on the soil of the cup. On the following day, the nymphs were sitting apathetically on the bottom and one of them on the cage. On 15.04. all were more or less motionless, some were laying on the side, and one perhaps dead. The same was observed on 17.04. with further two dead nymphs. Nothing of the provided herbs and grasses was eaten. Finally, only one nymph survived, first seen on 20./24.04. by nippling on *Trifolium* and *Plantago*, resulting in the first faeces. This strong juvenile *Prionotropis* finished the complete development over five instars in two months until mid-June (Table 5). The juvenile might have moulted sitting on the bottom, based on finding the exuviae beside the grasshopper on the ground (Fig. 6a). The single *Prionotropis* female was mostly immobile during day-light. The faeces were typically for Pamphagidae showing a ripling structure (Fig. 6b), and in dependence on the food varied from light brown to nearly black colour, measuring in N5 (03.06.23) 5.3-6.2 mm × 2.1-2.5 mm, and in the adult female 7.4-9.0 mm × 2.7-3.3 mm.

Additional length measures of N1 (2 ♀♀, 4 ♂♂) died after hatch (Nr. 80) and conserved in ethyl alcohol: body 6.2-7.5 mm, pronotum 2.0-2.5 mm, and postfemur 4.2-4.7 mm.

Table 5: Developmental duration of a single *Prionotropis* female and temperatures during caging (logger establishment, selection and computation by C. Schulze). Measurements of exuviae (N1 – N5, in mm) with an electronic caliper under a stereomicroscope.

Parameter	Hatch	N1	N2	N3	N4	N5
Date (2023)	28.3.-12.4.	13.4.-2.5.	3.5.-7.5.	8.5.-17.5.	18.5.-29.5.	30.5.-12.6.
Duration	16 d	20 d	5 d	10 d	12 d	14 d
Temperatures (°C)						
T-Ø	19.0	21.7	22.8	24.1	24.1	25.7
T_max	30.6	30.7	31.2	41.3	39.2	41.5
T_min	14.8	16.0	18.6	19.3	19.2	20.5
Exuvia size						
Postfemur (mm)	-	4.5	5.7	7.0	9.8	14.1
acc. Defaut & Morichon (2015)		4.3/4.5	5.5/6.3	7.8/8.3	9.4/12.7	13.3/17.6
Pronotum (mm)	-	1.8	2.5	3.6	7.2	10.5
Tegmen (mm)	-	0.6	0.7	1.2	1.9	3.5
Wingpads directed	-	ventrally	ventrally	ventrally	dorsally	dorsally

Adult female

After final moult (12.06., Fig. 6a) the adult female survived over three months until 09.09.2023. In the cage until mid-July a small container, later a flat dish with a dry/moist sand/soil-mixture was provided for egg-laying together with a large stone. As preferred food only *Taraxacum* and *Plantago* were provided and eaten when fresh. Like the juvenile, also the adult female stayed mostly immobile, only from time to time feeding on the herb leaves on the bottom. The typical damage is feeding on the leaf margin (on the base, in the middle or on the top), sometimes also separating the leaf in two parts (Fig. 6c).

According final control, this female produced 4-5 egg-pods, with one egg-pod every two to three weeks. Unfortunately, this occurred mostly not into the soil or under the stone, but the eggs were laid within an orange foam in the edges of the cage, which rapidly hardened and the eggs dried (Table 6). Only one time egg-laying behaviour was observed, where the female stretched its abdomen below a great stone. The average temperature amounted from 23.06.-06.07. to 27.3 °C, from 23.06.-11.09. (whole adult period) to 27.0°C and from 16.08.-11.10. (final egg-laying) to about 26.0°C. Therefore, no intact egg-pod resulted for further rearing, so far finishing the rearing study mid-October 2023 after about one year.

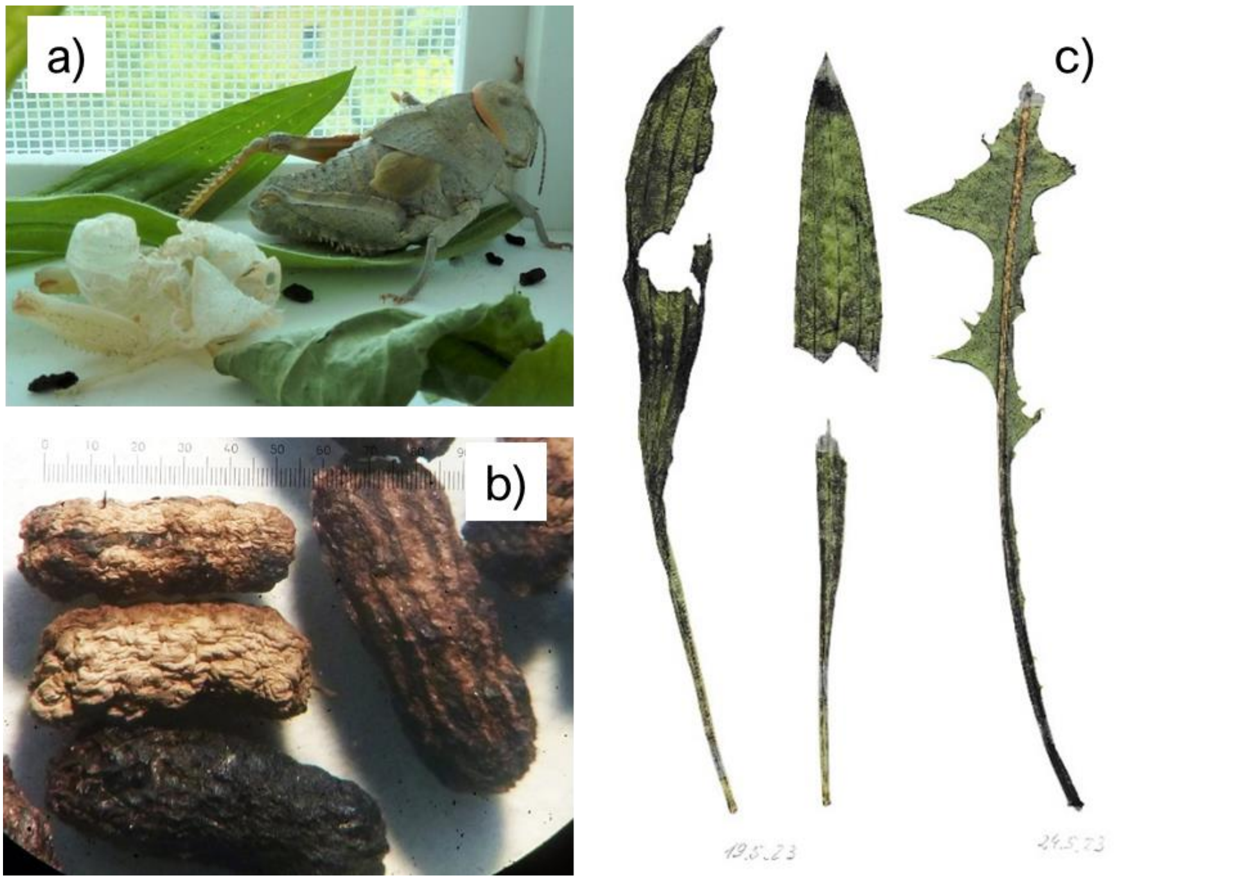

Fig. 6: a) Adult female after moult beside their exuvia, 12.06.2023; b) faeces of a young adult female of *Prionotropis*, fed with *Plantago* and *Taraxacum* herb leaves, 23.06.2023; c) feeding damage of *Prionotropis* (N4-♀) on leaves of *Plantago lanceolata* and *Taraxacum officinale*. Photos: Günter Köhler.

Table 6: Adult female of *Prionotropis* over their lifetime.

Date (2023)	07.07.	10.07.	27.07.	16.08.	8.-10.09.
Egg-pod	few foam in cage edge	on base of the sliding door	between dish and gauze	observed egg-laying below stone	in sand/soil-mixture
Egg number	3-5	15 (glued in foam)	few hardened eggs		2 egg-pods with 6/0 eggs
Feeding on	*Taraxacum officinale* and *Plantago lanceolata*				
Female (mm)	Body 41.7	Postfemur 19.0	Pronotum 13.5	Forewing 7.3	
acc. Defaut & Morichon (2015)	Body 42-48	Postfemur 17.8-22.2	Pronotum 14.1-15.7	Forweing 9.7-11.4	

Discussion

The decline of the endemic Crau grasshopper is mainly explained by habitat destruction and fragmentation in the last decades. But populations have also declined in protected areas, indicating that aspects of life history are involved. The results presented in this study, which is mainly based on eggs, can only partly support this hypothesis. In general, the life history of pamphagid species is still poorly understood, and only few studies were found that examined the entire life cycle (including eggs) of a pamphagid species (Shulov 1956, 1962).

In *Prionotropis* the fecundity of a female (here with Ø 70 eggs) seems to be high enough to resist population extinction, assuming an univoltine cycle. So far known, diapause (after a summer in the field) starts on a late embryonic stage around 80% of development. Obviously, after hibernating a distinct percentage of eggs did not develop further with embryos stagnating still in a late katatrepsis, indicating partly a two-year-cycle. According to the results, eggs are rather resistant against winter drought (which in reality seldom occurs). After that, and with water supply, they take off some amount of water, independently of embryonic development. In contrast to this, the eggs of the pamphagid *Tmethis pulchripennis* hatched completely (and only) without any addition of water, with a similar egg weight after oviposition, at the end of anatrepsis, and a slightly lower weight before hatching (Shulov 1952). If this is also the case for *Prionotropis*, any water supply (as well as early summer rain in the Crau) should stagnate the embryonic development, explaining at most the low hatching success in the laboratory, in addition to captivity or experimental effects. If the eggs of *Prionotropis* are not affected by water supply, then some eggs should overlay again one summer with some mortality until the next year. Furthermore, also juvenile mortality was high, which could be caused by too low rearing temperatures. Summarizing that, and if there are not only captivity effects, these three processes (partly bivoltine cycle, low hatching success, high first instar mortality) could decisively decrease small *Prionotropis* populations in the wild.

Acknowledgments

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