Self-rubbing of psammophiids


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Notes of the author

1. This article was originally submitted to Salamandra, but the editors did not want to accept it in this form for publication. The reasons they gave, were: the article was too long, too aggressive and too full of subjective statements. I did not “stick to the facts”. Instead of mutilating my article, I chose to withdraw it and publish it on the internet.

2. This article is partially based on the critical review of a thesis of S. de Pury about the rubbing behaviour of psammophioid snakes, that the author wrote together with Michel-François Habersaat, and that is published on the internet too.
Introduction

In *Salamandra* 49(1), 2013, Dr. STÉPHANIE DE PURY and Prof. Dr. WOLFGANG BÖHME published 'A contribution to the understanding of the self-rubbing behaviour in psammophiid snakes (Squamata: Psammophiidae)', in which they try to clarify some aspects of the self-rubbing behaviour of psammophiids snakes and discuss its possible functional significance. They conclude that the rubbing of these snakes "serves primarily the prevention of evaporative water loss" (p. 28). In that respect, their article seems to consolidate an interpretation of the self-rubbing behaviour that has been repeated in literature since it was developed by DUNSON, DUNSON & KEITH (1978).
I think this is a mistake.

The body water loss prevention interpretation of self-rubbing behaviour

In the description of the hypothesis that the self-rubbing of psammophiids snakes serves to protect the skin against water loss, the authors state: "... several authors considered selfrubbing as protecting the skin against water loss (BRANCH 1988, LAHAV & DMI’EL 1996, WELDON et al. 2008)" (p. 19).
In this short list of references, the field guide of BRANCH (1988) can hardly be called a serious source: he only mentions very shortly and inaccurately the self-rubbing behaviour in the general paragraph about sand and grass snakes: "Some species (*P. sibilans* and *P. schokari*) 'polish' themselves with a nasal gland secretion which reduces skin water-loss" (p. 70), without reference.
The second source, LAHAV & DMI’EL 1996, does surprisingly not even mention the rubbing behaviour. To the contrary, what these authors do write (see below), can be considered as an argument against the water loss hypothesis. As for the last source mentioned by DE PURY & BÖHME, there has also been some careless referring: WELDON ET AL. (2008) consider concerning psammophiids not only the water loss hypothesis: "Nasal gland fluids, which dry to form to a lusterless film on the skin, are hypothesized to retard evaporative water loss or to contain pheromones used to scent-mark conspecifics and/or territories" (p. 747).
WELDON ET AL. (2008) refer exclusively to DUNSON ET AL. (1978), including DUNSON’S incorrect suggestion that psammophiids "rub their snout along their dorsal and ventral skin surfaces" (p. 747), which DUNSON ET AL. on their turn borrow from DE GRIJS (1898), who observed P. sibilans and P. schokari but apparently not very closely. As we know, they only rub their ventral scales (except for *Rampphiopis* that also has been observed to rub lateral scales), and absolutely not their dorsum (see e.g. DE HAAN 1982, 1999; STEEHOUDER 1987; DE PURY 2010; videos as mentioned in the Reference List).
WELDON ET AL. (1978) refer to "watery nasal gland secretions", which is interesting in the context of a water repelling function of the same secretion. They also mention many other functions of chemicals in and from the skin: "Chemicals from the integument – the epidermis and skin glands – also protect reptiles against pathogenic microorganisms, ectoparasites, including disease vectors, and predators, in addition to attracting mates and eliciting other pheromonal responses."
It may be clear that WELDON ET AL. (1978) consequently can hardly be used as a backing for the water loss hypothesis. Even DUNSON, DUNSON & KEITH (1978), the original source of the water loss hypothesis, is doubtful, as was elaborately indicated by DE HAAN (1999). I have the impression all other authors that refer to this article, only read the abstract. In the body itself, the authors are much more careful. There is no indication that they themselves ever observed any rubbing
behaviour. Those snakes that were kept alive during their research, were kept in experimental conditions that make it rather improbable they ever rubbed. The experiments that were carried out to determine their evaporative water loss, did not include a comparison between snakes that had rubbed and snakes that had not. And yet, without rubbing, water loss was extremely low. "Indeed it may have the lowest rate of loss ever measured for an ophidian" (p. 472). And: "Under lab conditions (low activity, 24-27°C) *M. monspessulanus* does not need to drink to maintain its body weight. Sufficient water can be obtained from mammalian prey (lab mice are 73% water)" (p. 470). They conclude: "It might seem unlikely that small amounts of a substance spread over a snake's skin could have any significant effect on water permeability. [...] Since the chemical composition of the fluid is only partially known, nothing definite can be said about its ability to retard passage of water across the skin. However the well established property of certain compounds, such as cetyl alcohol and long chain fatty acids applied in monolayers, to considerably retard evaporation from water surfaces provides a useful model" (p. 472). A useful model for further research, that's all.

Apparently, DUNSON, DUNSON & KEITH (1978) do not take into consideration any other possible function of the secretion, which seems remarkable. Can this be the reason why DE PURY from the beginning (her 2010 dissertation) seems to have been fixated on, firstly, the presence of lipids in the secretion and, secondly, on the possible water repellent function of lipids in the secretion?

It is in my opinion obvious that DUNSON's hypothesis that smearing a watery secretion in a relatively narrow track only on the ventral scales (where it has the largest chance of being rubbed off in a short time by contact with the substrate) would be able to prevent water loss through the skin, must in fact be considered as extremely unlikely, and I find it remarkable that DE PURY & BÖHME remain so persistently fixed on that hypothesis.

DE PURY & BÖHME state: "This hypothesis received further support from some anecdotal reports that self-rubbing frequency was lower when the snakes were exposed to higher humidity (STEEHOUDE 1992, BRANDSTÄTTER 1996) and became higher when snakes were exposed to higher temperatures and drier conditions (DAREVSKY 1956, RIEPEL 1973, DE HAAN 1982, STEEHOUDER 1987, 1992)" (p. 19).

However, the authors do not consider any other explanation. I myself (STEEHOUDE 1991) for instance, suggested (assuming that the rubbing would serve to mark environment) that less rubbing would take place in non-arid conditions because in such an environment scents will evaporate and disappear at a slower rate, resulting in less need to refresh the traces. Also unproven, of course, but much more likely than the moisture loss hypothesis, as could be concluded from the study of ALBERTS (1992) and WYATT (2003).

The relation between high temperatures and water loss seems complicated in psammophiids snakes.

LICHT & BENNETT (1972) demonstrated the general ability of snake skin to protect against evaporation. LAHAV & DMI'EL (1996) discovered extremely low cutaneous water loss in experiments with *Psammophis schokari*, at low and at high temperatures, the lowest in the stripeless form of *Psammophis* from xeric biotopes in the Negev desert. The desert form of *Psammophis* appeared able to conspicuously change the values of cutaneous water loss. The authors think it likely that this "reflects peripheral vasomotor changes, i.e., vasodilatation and vasoconstriction of the skin blood vessels. Due to its diurnal activity, the xeric form of *Psammophis* is often exposed to intense solar radiation, high temperatures and low humidity common in deserts. Presumably, the vasomotor response enables this snake a better and more immediate control of its CWL" (p. 138).
Some psammophiids inhabit environments that are not so dry after all, for instance *Psammophilis (Dromophis) lineatus* that typically inhabits wetlands (Biodiversity of the Zambezi Basin Wetlands 2000). Still, these also exhibit rubbing behaviour. It would be worth considering this aspect too.

If De Pury & Böhme want to seriously defend the so unlikely water evaporation hypothesis, against all odds, one would expect a very serious research. I was rather disappointed when I read their paper. For instance: they analysed the ultrastructure of dorsal and lateral scales. In the article in *Salamandra* they don't tell us why, but reading the 2010 dissertation of De Pury makes clear that this serves to investigate if the ultrastructure of psammophiids scales differs from those of other snakes in a certain aspect, that is the absence of pores. "… if psammophiids have a porous structure to allow the exit of lipids (...), why should they additionally smear a secretion containing lipids on their body?" (par. 1.7a).

This is a rather strange motivation, as it already assumes what yet has to be proven: that the secretion contains lipids that can and do protect the snake's skin against water loss. And what is more: if there would have been pores, this would not necessarily have meant that the (hypothetical) lipids would NOT have acted as an additional protection. And thirdly: if there were pores, would they serve as secreting ducts for lipids? And finally: what proof would there be that the found lipids would serve to prevent water loss and not have any other function, for instance pheromonal?

But my most obvious objection is: why didn't the authors analyse the ventral scales, as these are the scales that are rubbed and smeared? Instead, they analysed vertebral and lateral scales - that are not rubbed at all. Only *Rhamphiophis* sp. seem to rub lateral scales, all other species only rub the ventral scales. Readers that never have observed the rubbing behaviour of these snakes, can easily see what I mean if they look at the videos I placed in my Youtube Channel (address added to the list of references). It is a pity that the videos that were used in the research of De Pury & Böhme are not available for public use.

Considering the above, the analysis of the scales as described in the paper of De Pury & Böhme, seems interesting but in this context rather irrelevant, as is consequently everything the authors state about it in their discussion section. From the 2010 dissertation of De Pury, where the research is more elaborately described, I learned that the lateral scales have been left out of further research from the beginning, as there appeared to be very little structure on their surface (De Pury 2010, par. 3.1). The ventral scales (which, I repeat, are the only scales that are rubbed) almost completely lack surface structure, except for a short period after shedding (Brandstätter 1995). The authors state on p. 26: "With regard to rubbing behaviour, the delicately sculptured micro-ornamentation might serve to retain the nasal glands’ secretion on the scale surface". What is there to retain if the secretion is not even applied to these dorsal scales? Only if this retaining would concern secretion that was rubbed off from the belly of a snake to mark another snake, would the remark be sensible, but that seems not to be the intention.

I can be short about the analysis of the secretion that is described and discussed in the article of De Pury & Böhme: absolutely nothing can be concluded. "The presence of lipids in the nasal secretion could be clearly determined in the two species studied. However it could not be clearly identified which lipids exactly they are" (p. 27). Neither was there any clue to what the function of the unknown lipids could be.
In the study of Dunson, Dunson & Keith (1978) lipids were also found in the secretion, but only in small quantities: "The lipid content of the secretion appears to be a very minor component" (p. 468). There is no indication for the relative quantity of lipids De Pury & Böhme have found. The rest in Dunson's samples were mainly proteins, which is according to the findings of De Haan (pers. comm.) in the 1980's and even in the late 1960's, who had samples of dried secretion that was scraped off a front glass panel (see above) gas chromatically analysed. Proteins do often have a pheromone function - as do lipids and fatty acids (Wyatt 2003).

Dunson, Dunson & Keith (1978) stated: "The task that remains is to collect the natural secretion and to directly test its effect on skin water permeability". This was apparently not possible within the boundaries of the research of De Pury & Böhme.

The reference to the rubbing behaviour of some frogs (p. 28) is not very convincing. Dunson, Dunson, Dunson & Keith (1978) already pointed to the superficial similarity with the rubbing of Malpolon, but admit that in the frog secretion lipids were dominantly present, but "that the nasal secretion of M. monspessulanus contains fatty acids and the skin surface in snakes is considerably more keratinized" (p. 472).

In short: the analysis of the scale structure and the secretion involved, as described in the article of De Pury & Böhme, proves interesting but in my opinion completely fruitless. The main conclusion seems to be that nothing could be concluded.

Following Licht & Bennett (1972) who concluded that the presence of scales has nothing to do with the evaporative water loss through the skin, De Pury & Böhme state: "Indeed, the protective mechanism of the skin against water loss lies in the epidermal layer of the skin and not on its surface" (p. 26). Apparently the authors and I agree that the analysis of the scale structure and of the secretion did not support the water loss hypothesis in any way. Lipids play a role in the prevention of water loss in snakes, but they seem to do so in the skin tissue, not applied on its surface - at least, there is not a single indication that this would be the case, neither in the literature cited by the authors, neither in their own research.

The chemical marking interpretation of rubbing behaviour

Considering my foregoing objections, it may be clear that I think that the hypothesis that the self-rubbing serves as prevention of water loss will probably never be confirmed, and that another explanation can only be more plausible. Such an other interpretation of the rubbing behaviour is that self-rubbing is used to mark substrates, territories and conspecifics, as is extensively argued by De Haan (1982, 1999, 2003) and De Haan & Cluchier (2006).

This hypothesis is also the one that is the most likely. The analyses of Darevsky (1956), Dunston, Dunston & Keith (1978) and of De Pury & Böhme (2013) all show the presence of chemicals that are commonly used in or as pheromones (see Wyatt 2003). As far as lipids are concerned: "The signal life of mammalian pheromones used as territory markers was increased by carrier components in secretions such as sebum, a lipid-rich, oily substance produced by sebaceous glands" (Wyatt 2003).

In the section of the 2013 article by De Pury & Böhme in which the behavioural experiments are described and discussed, the authors try to find indications that would falsify or confirm De Haan's marking interpretation. The original dissertation that has been the basis of the 2013
article, even had a working hypothesis that 'Rubbing behaviour is not a marking behaviour" (par. 1.7 of the dissertation).

The observations in the behavioural experiments as described in the dissertation and in the 2013 article, are very interesting. It is a pity that not more results of the observations of rubbing behaviour from the 2010 dissertation have been included in the 2013 article. However, a major objection is, that all animals involved were observed in conditions that were totally different from their natural: in small enclosures that were temporarily inhabited, solitary, sometimes placed in a new enclosure and removed within some hours. It is not at all clear to what extent observations made in such circumstances can be applied to normal behaviour in natural circumstances. De Haan (1999, 2003) observed Malpolon in semi-natural circumstances, in wide open enclosures in an area that belongs to their natural habitat. Comparisons should thus be very carefully made.

The description of the experiments of De Pury & Bohme is unfortunately incomplete. For instance: it is stated that continuous recording was chosen so that the animals would not be disturbed (p. 20), but exactly how undisturbed were they? De Haan (pers. comm.), Haddersaat (pers. comm.), Steehouder (unpubl.), they all observed that the rubbing behaviour was strongly influenced by the presence of observers. The animals that were kept in enclosures in a room almost only rub when they feel safe and are not disturbed by the sight of people moving through the room or watching them. When they have started a rubbing session, they almost always stop when an observer comes in sight. The 2013 paper of De Pury & Bohme and the 2010 dissertation do not fully describe the circumstances under which the animals were observed. What we do know is, that in part of the experiment there has been a lot of manipulating of the animals involved. That decreases the reliability of the observations.

De Pury & Bohme tried to determine whether there would be a difference in frequency in rubbing behaviour, assuming that marking behaviour would be activated if the animals were put in a clean, new environment. Their data did not confirm this assumption. "Rubbing frequency was not significantly higher on the first day than during the following days in the 15 psammophiids tested" (p. 24).

Anecdotal data from Schach (pers. comm.) and myself seem to contradict the observation of De Pury & Bohme. And what to do with the remark of the authors themselves on p. 21: "Our preliminary experiments had shown that RB is mainly performed during the first 60–90 minutes after being placed into a new terrarium"? The authors do not try to explain the deviation between expected and observed behaviour.

On the other hand, the assumption in itself is also disputable, as it is based on a narrow interpretation of the hypothetical marking behaviour, viz. that it serves to mark a territory, and that without a spatial, environmental or social context. It is not sure that being placed in a absolutely clean and new enclosure, without traces of conspecifics or other snakes would specifically elicit rubbing behaviour.

De Haan (2003): "In Malpolon monspessulanus, a species showing pronounced sexual dimorphism […] I observed chemical marking with ventrally scraped off nasal secretion particles [15,19]:

- of hunting routes traced on substrate by all individuals, irrespective of sex and age;
- of conspecifics in holes and other dark places, where the marking afterwards serves for mutual recognition, prevents panic and favours clan formation, but might also discourage aggregation since given individuals risk becoming the prey of opportunist conspecifics;
of individual territory limits traced upon and between optical landmarks by certain adult males, limits which they guard and defend as well as their respective females against most male conspecifics and diverse allospecific intruders during 6–8 weeks in May/June;

- by a territorial male, marking his female and one or two vassal-males, which also – if not mainly – mark themselves dorsally by frequently creeping under the territorial dominant."

If De Haan is right, the marking behaviour is much more complex than simple marking of a territory. There could also be a connection with a neglected element in the study of Dunson, Dunson & Keith (1978), who found that "Different samples showed considerable variation" (p. 467). Dunson, Dunson & Keith (1978): "A major portion of the central area of the gland is an extensively branched system of ducts. In the only previous study of the gland, there was no mention of this peculiarity (Darevski, '56). The need for such an enormous system of ducts remains unknown, but it is likely that in addition to storing and passing the fluid released by the tubules, the ducts have an active role in determining the final composition of the secretory fluid (p. 471)."

So it is not clear if the composition of the secretion is always the same, and it would be possible that it differs according to the actual function of the rubbing.

Another part of the experiment of De Pury & Böhme consisted in the use of glass plates over which the animals crawled. Horizontal glass plates were used, over which the animals were intended to crawl, rubbing off the secretion that had been applied in a rubbing session.

"None of the individuals of both species studied had left visible traces of secretion on the glass plate" (p. 24). I think it would have been very unlikely if they had. The article does not describe exactly how the glass plates were observed: with or without a microscope? 'Visible' suggests that it has been done without. But even with the help of a very good microscope, it would have been very hard to find particles (presumably scraped off, in this case on smooth glass) forming a scent trace. This part of the experiment seems to assume that large quantities of the secretion, visibly observable, would be needed to mark a trace. A very strange idea, if we only remember how a dog is able to follow a trace or is able to detect a corpse from a distance. Just as an example: dogs are able to detect 80% of some materials in densities of 100 particles per 1.000.000.000 (Settles 2005). Like a needle in a haystack! Why would be assume that these snakes would need such enormous quantities of particles that we would be able to see them even without a microscope?

Maybe there has been a confusion with the very visible traces of secretion these snakes often apply actively on the front glass panels of their enclosures by rubbing their nose against the panel (see picture 1). It is not clear if this is a deliberate and/or functional action. They can easily be scraped off for investigation, and then form a sticky material. The wipes can very easily be removed with a moist towel or paper. The water resistance seems low.
Temperature dependent?

In the last part of their article, the authors state: "The overall analysis of the 17 psammophiids investigated in the present study support the hypothesis that their rubbing behaviour depends on temperature …" (p. 28). The background of this hypothesis is of course, that higher temperatures mean more evaporation and, as we know, the authors wanted to find a connection between evaporation and frequency of self-rubbing. However, the relation between temperature and self-rubbing frequency in their data is not as impressive as they suggest. In the original dissertation of De Pury (2010) more details are given. Tables 3.5 and 3.6 in that dissertation show that in one Scutophis (Rhagerhis) moilensis there was a correlation, in three others not; in five Psammophis mossambicus there was, in one not; in two Psammophis schokari there was a correlation, but in two other ones not. Though there was an over-all correlation, the outcome of this experiment remains thus unclear, and the cases in which there was no correlation, should have been explained. Besides, other explanations would have been possible, apart from the one I mentioned in the above. In general, for instance, the animals become more active when temperature rises. It would be plausible that rubbing behaviour would be part of normal activity and become more
frequent. If one would want to find out if the frequency increase of rubbing behaviour is independent of a more general increase of activity, more data are needed.

**Conclusion**

De Pury & Böhme (2013) state: "The overall analysis of the 17 psammophiids investigated in the present study support the hypothesis that their rubbing behaviour depends on temperature and serves primarily the prevention of evaporative water loss" (p. 28). As for the first part of that conclusion: that remains to be investigated, and if so, there cannot simply be concluded that this has anything to do with evaporation. As for the second part of the conclusion, I honestly ask myself and the readers: where in the world is it based on? Let us not forget how very unlikely the water loss hypothesis is in the first place. Such a hypothesis would ask for a much stronger support than given in the paper of De Pury & Böhme, in which I find not even a shadow of proof.

We have seen that since 1978 (uncareful) reading of the study of Dunson, Dunson & Keith (1978) has led authors to jumping to the conclusion that the rubbing behaviour of psammophioid snakes serves to prevent body water loss. The article of De Pury & Böhme (2013) seems to perpetuate this incorrect conclusion. I hope my contribution has made sufficiently clear that this has to be considered a mistake.

The hypothesis of De Haan (1999, 2003, cf. De Haan & Cluchier 2006) that the psammophioid self-rubbing behaviour "serves as a preliminary to subsequent chemical marking of conspecifics, nest and hunting routes" (De Haan 2006) seems much more promising. De Haan seems convinced that this is at least the case for the Eastern and Western Montpellier snakes (resp. Malpolon insignitus and M. monspessulanus), most notably for certain males in May-June, but it could be hypothesised as a model to explain the self-rubbing behaviour of the other members of the psammophioid group.

Videos of rubbing psammophiids can be found on the internet, in the Youtube Channel of Ton Steehouder, [https://www.youtube.com/user/Ton19462/featured?view_as=public](https://www.youtube.com/user/Ton19462/featured?view_as=public), or through the link [http://Psammophis.nl/indexfilms.htm](http://Psammophis.nl/indexfilms.htm).

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