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Letter to the Editor

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Pellet egestion in modern carnivorous snakes

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Food resources vary in terms of digestibility and constraints in food processing are an essential factor driving the evolution of adaptations to cope with them, for example, a complex morphology of gastric tract, symbiosis with microorganisms, enzymatic specialization (McNab 2002). Pellet egestion is another important adaptation that enables to remove indigestible food particles and is observed in several vertebrate taxa. Pellets are most commonly reported in sauropsids, particularly birds, but published records indicate pellet formation also in the 2nd groups of sauropsids, that is, nonavian reptiles, including lizards and snakes (Myhrvold 2012). In snakes, pellet formation and egestion may, however, seem counterintuitive due to extreme digestive efficiency of snakes that allows them to process almost all prey tissues (Skoczylas 1970). In fact, pellets in snakes are reported mostly in fossil material (Myhrvold 2012), whereas in modern snakes pellets seem to be documented exclusively in ovivorous species (e.g., *Dasypeltis* spp. and *Elachistodon* spp.; Gans 1952). In carnivorous snakes, pellet egestion was only invoked by Myhrvold (2012) as a reference to Gans (1952). Surprisingly, the cited study of Gans (1952) does not mention nor document physiological pellet formation and egestion by carnivorous, but only ovivorous snakes. Therefore, observations of pellets in modern carnivorous snakes appear entirely lacking. Such observations could, however, provide substantial contribution to the comparative digestive physiology of vertebrates.

Here, we document probably the first empirical evidence for the pellet formation and egestion in modern carnivorous snakes. Observations were performed on captive groups of banded water snakes *Nerodia fasciata* ($N = 30$) obtained from private collection as juveniles (<6 months). All snakes were kept in standardized conditions, solitarily, with water container, photoperiod set at 12:12 h light:dark and ambient temperature on the level of 26°C–27°C (temperature preferred by *N. fasciata;* S. B. personal observation and Hopkins et al. 2004). Snakes were provided with dead hairless rodent pups once per week. Food was changed from pups to subadult rodents covered with fur as snakes were growing to size making them enable to ingest larger food particles. In one female (body mass: 23.4 g), 7 days after ingestion of a vole, prior next feeding, a compact mass of distinguishable shape was palpated. The location of the object in the mid-body at approximately half of the snout–vent length indicated its location in the stomach, which was further confirmed by the X-ray examination (performed in MedicaVet Veterinary Clinic, Cracow, Poland; Figure 1A). One day later the specimen was observed to eject orally a structure resembling avian pellet, that is, containing bones and fur, being dry and lacking any soft tissues (Figure 1B). Similar behavior was observed afterward in 7 other specimens. In total, pellet egestion was observed in 8 among 681 feeding events (~1%) within 6 months. These feeding events concerned 30 individuals of *N. fasciata*, among which 8 (3 males and 5 females; 26% of snakes) have egested pellets. In all cases, pellets occurred after 1st or 2nd feeding with vole covered with fur and were observed only once per individual. Each time pellets were egested after 5th-day post-feeding. Simultaneously, a group of field-caught European grass snakes *Natrix natrix* ($N = 51$) was maintained under similar captive conditions as banded water snakes. All specimens were adults and also fed with rodents, but due to larger size not with pups but subadult or adult voles. Among more than 1,200 feeding events over 6 months only once a structure resembling a pellet was found, however, it was not observed whether snake egested it orally or removed with feces.

We have controlled snakes' health, condition, and the environment, because egestion of food particles is commonly reported in association with digestive disorders, stress, and suboptimal temperature (Divers and Mader 2005). However, signs of such disorders, for example, gross swelling of the abdomen or diarrhea, were not observed. Snake that produced pellets did not express any symptoms of pain or stress, for example, ceased food intake (James et al. 2017) and fecal samples did not exhibit any signs of parasitic infestation. Furthermore, egestion of pellets seemed not to result from regurgitation or vomiting, both outcomes of incomplete digestion (Divers & Mader 2005). Vomited or regurgitated particles are non- or partially digested, usually floppy, wet, and still containing soft tissues contrary to those here reported (see above and

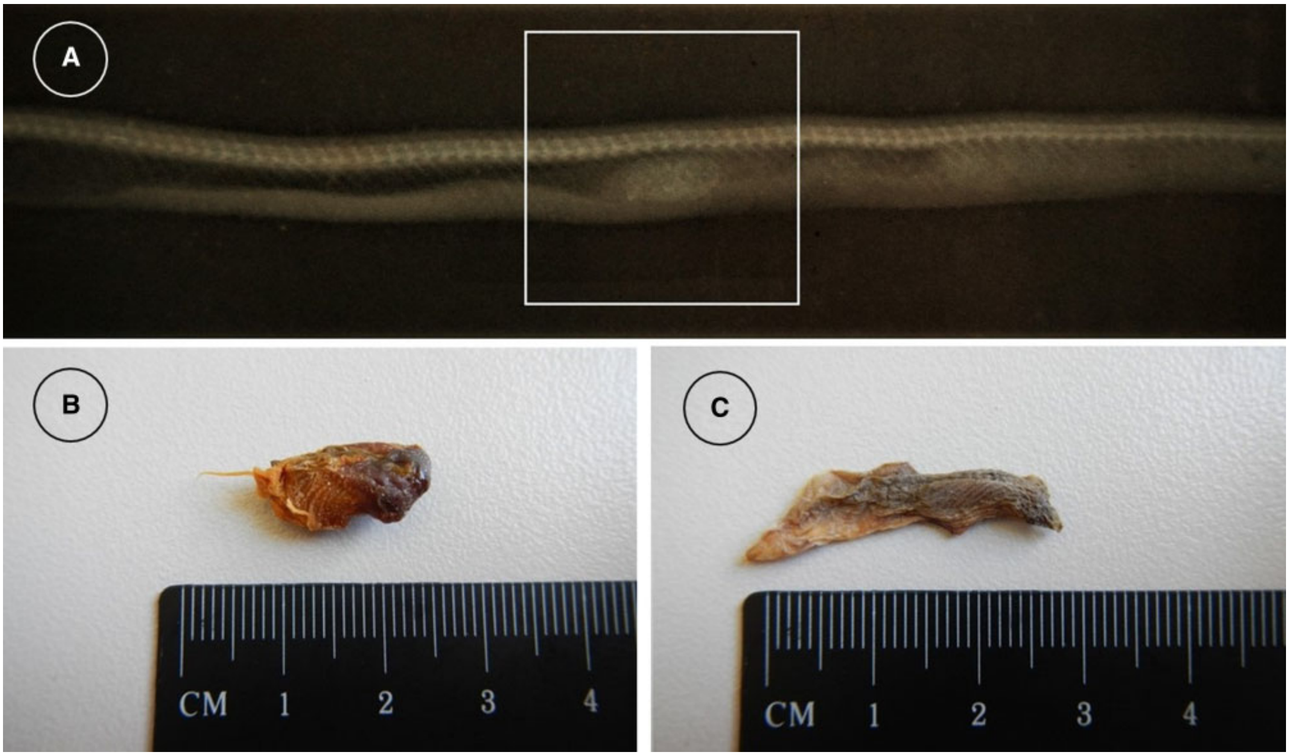

Figure 1. (**A**) X-ray of the snake with the first observed case of pellet located in the stomach (position of the structure is marked); (**B**, **C**) 2 exemplary pellets obtained from 2 different individuals (nondigested ribs of the prey are visible in both cases).

Figure 1B,C). Snakes were, however, kept in an optimal temperature that allows to complete digestion within ~3–5 days (Hopkins et al. 2004), whereas pellets were egested after such period, that is, after completed digestion. Finally, snakes that produced pellets did not differ in body mass (Mann Whitney *U*-test; $U = 50$, $N = 30$, $P = 0.13$) and growth rate (assessed over 1 month) from other specimens (Mann Whitney *U*-test; $U = 66$, $N = 30$, $P = 0.49$). In the case of grass snake, the one pellet-like structure found in the terrarium was unlikely to be removed with feces, since it was clean, and similarly as in *N. fasciata*, it was found after the digestion is completed (c.a. 3 days for *N. natrix* according to Skoczylas 1970). Moreover, such dry and hard-bodied structure would rather constipate intestines if not removed with feces.

Our observations clearly show that avian-like pellet formation and egestion do exist in modern carnivorous snake species. Similar structure was observed to be ejected in *Pseudocerastes urarachnoides*, but as a stress response toward handling (Fathinia et al. 2009). In our case, pellet egestion appears to occur in snakes without any digestive disorders nor as a stress response, thus we consider it as a physiological countermeasure of snakes to cope with indigestible food fraction. The observed phenomenon could have been overlooked so far due to its rare occurrence as here reported. Observed structures strongly resemble pellets reported in birds, that is, were egested after the digestion process was completed and were dry containing apparently indigestible food fraction, mainly bones, sometimes teeth, but without soft tissues (Grimm and Whitehouse 1963; Figure 1B,C). In each case, we observed pellets after switching the diet of snakes from vole pups to subadult rodents. This indicates that older prey imposes limitations to digestive performance, possibly due to more mineralized skeleton. This can be particularly marked in water snakes due to their dietary specialization toward fish (Hopkins et al. 2004). Indeed, dietary specialization was shown to affect digestive performance depending on the type of ingested prey (Britt and Bennett 2008). Interestingly, no similar observations were made on larger sample of grass snakes, also specialized in amphibians and fish (Skoczylas, 1970). However, grass snakes were field-collected, therefore likely to forage on wider spectrum of prey prior capture contrary to captive banded water snakes, fed on 1 meal type. We promote, that limited variation in diet composition, especially during development, may narrow the capacity and flexibility of digestion in snakes and this could appear particularly marked in dietary specialists (Britt and Bennett 2008). The phenotypic plasticity of digestive performance remains poorly studied in snakes, despite vast amount of data on digestive physiology, and should be covered by future studies. It is also important to get insight whether the mechanisms of pellet formation and egestion in carnivorous snakes resemble the processes observed in birds and ovivorous snakes. Further data on the pellet formation in other groups of sauropsids, besides birds and particularly in various taxa of non-avian reptiles could provide an insight into phylogenetic pattern of pellet formation and egestion.

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