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KERATOPHAGY IN REPTILES: REVIEW, HYPOTHESES, AND RECOMMENDATIONS

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ABSTRACT: Consumption of the whole or part of a reptile's own shed skin or that of a conspecific (keratophagy) has been documented in 248 species of lizards in 16 families and 19 snakes in four families. There are no authentic cases in turtles or crocodilians. An earlier review based primarily on zoo records noted keratophagy in 160 species of lizards, of which 16 were from literature sources designating field observations or stomach contents. We added an additional 16 captive observations for lizards and brought the total to 89 species for which this behavior has been documented in nature. Eating shed skins of conspecifics has been observed in 23 lizard species in five families. All of the 19 snake species known to have eaten their shed skins, except one, a *Clelia clelia,* were in captivity. We reviewed six hypotheses that may explain the occurrence and evolution of keratophagy. These are the Nutritional Hypothesis, Skin sensitivity hypothesis, Artificial Behavior Hypothesis in Snakes, Accidental Hypothesis, Predator Avoidance Hypothesis, and the Reduced Parasite Load Hypothesis. The Nutritional and Artificial hypotheses provide the least explanatory power for this behavior. The remaining four hypotheses have varying levels of predictability but each may function within different contexts. We provide recommendations for elucidation of these hypotheses in our discussions of them. Finally, our attempts at electronic searches were hindered because of the variation in the terminology used for this behavior, and because most authors did not include an appropriate term in their list of keywords or in the abstract. We recommend standardization of the term "keratophagy," and that authors of diet and behavioral studies in which consumption of shed skin was observed include this term in abstracts and key words.

KEY WORDS: behavior, keratophagy, lizards, snakes, turtles, predator avoidance, reptiles, shed skin.

INTRODUCTION

The consumption of shed skin has been observed in a broad taxonomic diversity of reptiles. It was first noted in *Anolis carolinensis* by Lockwood (1876) and Monks (1881). Although it is especially well known in geckos (M. A. Smith, 1935; Bustard and Maderson, 1965; Weldon *et al.*, 1993), it also occurs in other lizard groups and in some snakes (Groves and Groves, 1972). Literature references refer to this behavior as the consumption of an individual's own shed epidermis and occasionally as consumption of shed skin of one individual by a conspecific. The terminology for this behavior, however, has not been consistent. Groves and Groves (1972) introduced keratophagy, whereas other terms were used by Iverson (1979), Weldon *et al.* (1993), and Seipp and Henkel (2000).

Bustard and Maderson (1965) provided the first review of keratophagy in 17 lizard species and Weldon *et al.* (1993) extended the taxonomic coverage from observations provided by a large number of zoos and reached a total of 153 species. Mattlin (1946) was the first to describe a snake eating its own skin. Groves (1964) and Groves and Groves (1972) published occurrences in an additional four species. Kuch (1998) brought the total to eight. We expand the review of this behavior in reptiles and add additional information that allows generation of hypotheses. Unless otherwise noted, our review includes observations of individuals eating their own shed skin. In cases where

the information available indicates only that the behavior was recorded, we use the terms "captivity" and "field" to specify the environmental conditions in which it occurred. We present our information in three ways. (1) We list new, simple observations of keratophagy in captivity to add to the list in Weldon *et al.* (1993) for lizards and those in Groves and Groves (1972) and Kuch (1998) for snakes. (2) We include all literature available to us in which observations of this behavior were documented in the field whether published previously or not. This includes notes of "shed skin" in tables on a species' diet diversity. (3) We provide details of observations noted in the literature on consumption of shed skin from a conspecific by another individual. Higher order taxonomy follows Zug *et al.* (2001) and Han *et al.* (2004). Our aim in this paper is to provide an updated review of species performing this behavior, examine new and published hypotheses on its causes and benefits, and suggest recommendations for testing these hypotheses.

Results

Reptilia: Squamata

Lacertilia

Agamidae

Hydrosaurus amboinensis – Lederer (1929) observed captives eating the shed skin of conspecifics.

Physignathus cocincinus – Captivity (J.B. Murphy, pers. comm.).

Sitana ponticeriana – Sharma (2002) found shed skins in several stomachs, although it is not clear if they were their own skins or those of others.

Uromastyx acanthinura – Captivity (R.E. Honegger, pers. comm.).

Anguidae

Celestus agasepsoides – Shed skins were found in the stomachs of 41 field-caught specimens (White *et al.*, 1992).

Elgaria coeruleus – Fitch (1935) found tail skin in a wild-caught individual.

Ophisaurus ventralis – Shed skin was found in the stomach of a field-collected specimen (Palmer and Braswell, 1995).

Wetmorena haitiana – Two of 22 wild-caught individuals contained shed skin (Cizek *et al.*, 1990).

Chameoleonidae

Chamaeleo namaqueisis – Captivity (Burrage, 1973).

Carphodactylidae

Nephrurus levis – Captivity (Wagner and Lazik, 1996).

Cordylidae

Gerrhosaurus flavigularis – Shed skins were found in field-collected specimens (Loveridge, 1936, 1942).

Zonosaurus madagascariensis – Captivity (J.B. Murphy, pers. comm.).

Eublepharidae

Aeluroscalobotes felinus – Captivity (J. B. Murphy, pers. comm.).

Coleonyx variegatus – captivity (Cope, 1900; J.D. Groves, per. obs.). Klauber (1945) observed captive geckos detach and eat their own slough and that of conspecifics. Parker and Pianka (1974) recorded four of 185 wild-caught specimens with shed skin in their stomachs. They regularly eat their sloughs, if not always (J.D. Groves, pers. obs.).

Diplodactylidae

Diplodactylus (Strophurus) elderi – Bustard and Maderson (1965) observed juveniles eating their shed skin in the wild.

Oedura marmorata – Bustard and Maderson (1965) observed juveniles eat shed skin in the wild.

Oedura monilis – Shed skin was found in stomach contents of a field-collected specimen (Bustard and Maderson, 1965).

Oedura tryoni – Bustard and Maderson (1965) observed juveniles eat shed skin in the wild.

Rhacodactylus auriculatus – Four of 19 field-caught specimens had shed skin in their stomachs (Bauer and Sadlier, 1994). Seipp and Henkel (2000) noted that *Rhacodactylus* spp. usually swallow their shed skins completely, even freshly-hatched young.

Gekkonidae

Afrogecko porphyreus – Bustard and Maderson (1965) observed juveniles eat shed skin in the wild.

Bavayia sauvagii – Shed skin was found in 8 of 8 field-caught specimens (Bauer and DeVaney, 1987). [Diplodactylidae]

Chondrodactylus angulifer – One of four specimens collected in the field contained shed skin (Bauer *et al.*, 1989).

Christinus marmoratus – Bustard and Maderson (1965) observed juveniles eat shed skin in the wild.

Gehyra australis – Large portions of shed skin have been found in wild caught specimens (Bustard and Maderson, 1965).

Gehyra variegata – Large portions of shed skin have been found in wild caught specimens (Bustard and Maderson, 1965).

Gonatodes humeralis – Vitt *et al.* (1997a) found shed skin in stomach contents of field-collected specimens. Shed skin was found in 4 of 124 field collected lizards (Miranda and Andrade, 2003).

Gymnodactylus geckoides – Shed skin was found in 10 of 370 wild lizards (Colli *et al.*, 2003).

Hemidactylus frenatus – Taylor (1963) observed a neonate consume its first shed skin in the field.

Auffenberg (1980) noted that gecko skin was often found in their stomachs.

Hemidactylus haitianus – Noble and Bradley (1933) reported that captive adults and hatchlings were observed eating shed skin of conspecifics.

Hemidactylus turcicus – Three shed skins were found in 167 field collected specimens (Saenz, 1996).

Homopholis wahlbergii – Captivity (D.G. Broadley, pers. comm.).

Nactus pelagicus – Shed skin was noted in the stomach of a single field-caught specimen (Bauer and DeVaney, 1987).

Nactus serpeninsula – Vinson (1975) recorded that one of eight wild-caught adults contained an entire shed skin.

Pachydactylus geitje – Bustard and Maderson (1965) observed juveniles eat shed skin in the wild.

Ptenopus garrulus – Shed skin was found in 2.6% of 640 wild caught specimens (Hibbitts *et al.*, 2005).

Tarentola annularis – Loveridge (1947) noted that captives carefully peeled shed skin off their limbs like a glove and ate it.

Tarentola mauritanica – Gil *et al.* (1994) found shed skins in stomach contents of field-collected specimens.

Teratoscincus scincus – Captivity (J.B. Murphy, pers. comm.).

Thecadactylus rapicauda – Shed skin was noted in stomach contents of field-collected specimens (Vitt and Zani, 1997).

Iguanidae

Amblyrhynchus cristatus – On several islands in the Galapagos, J.D. Groves observed skin passed in feces and ingestion of lizard's own skin, mostly from the legs and dorsum and lateral surfaces of the body.

Anolis amouri – Shed skin was found in 5 field-collected lizards (Lenert *et al.*, 1994).

Anolis carolinensis – Hamilton and Pollack (1961) noted that two of six field-collected anoles contained parts of their own shed skin. Lockwood (1876) and Monks (1881) described keratophagy in captive specimens. Greenburg (1978) provided a photograph of social grooming in which one lizard is eating the shed skin of another.

Anolis chrysolepis – Vitt and Zani (1996) noted shed skin in stomach contents in field-collected specimens.

Anolis cristatellus – Captivity (Spieler, 1946). Shed skin is common in stomachs of field-collected specimens (Wolcott, 1924; Fitch *et al.*, 1989).

Anolis equestris – Captivity (Petzold, 1982). Four of five wild individuals contained shed skin (Herrel and O'Reilly, 2006).

Anolis garmani – One of 31 wild specimens examined by Herrel and O'Reilly (2006) contained shed skin.

Anolis longitibialis – Five of five field-collected individuals contained shed skin (Gifford *et al.*, 2002).

Anolis porcatus – Meshaka *et al.* (1997) found shed skin in stomach contents of a field-collected specimen.

Anolis limifrons – Field observation only (R. Andrews, pers. comm. to J. D. Groves).

Anolis nebulosus – Jenssen (1970) observed removal and ingestion of shed skin by anoles in natural populations.

Anolis nitens – Shed skin was found in one of 184 wild-caught specimens (Vitt *et al.*, 2001).

Anolis oxylophus – One lizard contained a complete skin, presumably his own (Vitt *et al.*, 1997b).

Anolis recordii – Captivity (Petzold, 1982).

Anolis roquet – Wingate (1965) recorded one specimen of 30 with its shed skin or that of a conspecific in its stomach.

Anolis sagrei – Field observation (Losos and de Queiroz, 1997).

Anolis trachyderma – Shed skin was found in nine of 180 wild-caught specimens (Vitt *et al.*, 2002).

Callisaurus draconoides – H.M. Smith (1946) noted shed skin in a presumably field-collected specimen. Pianka and Parker (1972) found shed skin in 13 of 469 wild-caught specimens.

Cophosaurus texanus – Durtsche *et al.* (1997) found shed skin in stomach contents of a field-collected specimen.

Ctenosaura similis – Captivity (J.B. Murphy, pers. comm.).

Cyclura carinata – Iverson (1979) recorded that 12 of 54 individuals had skin fragments in their stomachs and that a female contained a male's dorsal spine.

Cyclura cychlura – Murphy (1969) observed captives pull shed skin from conspecifics and then eat it.

Enyalius bilineatus – One of two wild-caught specimens examined by Vanzolini (1972) contained its own shed skin.

Enyalius brasiliensis – One of 14 wild-caught lizards contained shed skin (Van Sluys *et al.,* 2004), and one of 89 contained had shed skin in its stomach (Teixeira *et al.,* 2005).

Enyalius leechii – Shed skin was found in stomach contents of field-collected specimens (Vitt *et al.,* 1996).

Holbrookia propinqua – Judd (1976) found shed skin in one of 101 specimens.

Leiocephalus barahonensis – Shed skin was found in five field-collected lizards (Micco *et al.,* 1997).

Phrynosoma cornutum – Shed lizard skin was noted in the stomach of one of 10 field collected specimens (Lemos-Espinal *et al.,* 2004).

Phrynosoma modestum – Shed skin was noted in the stomach of one of 12 field collected individuals (Lemos-Espinal *et al.,* 2004).

Phrynosoma platyrhinos – Pianka and Parker (1975) noted that shed skin was found in field collected specimens from throughout its range.

Polychrus acutirostris – One field-collected specimen contained its own shed skin (Vitt and Lachner, 1981).

Sceloporus undulatus – One of 60 field-collected fence lizards contained shed skin in its stomach (Hamilton and Pollack, 1961).

Tropidurus hispidus – One of 23 wild caught specimens contained shed skin (Van Sluys *et al.,* 2004).

Tropidurus montanus – Two of 32 wild caught specimens contained shed skin (Van Sluys *et al.,* 2004).

Uma notata – Carpenter (1963) observed captive individuals eating their own shed skin and that of conspecifics.

Uma paraphygas – Gadsden and Palacious-Orona (1997) found shed skin in stomach contents in one of 19 field-collected specimens.

Uma scoparia – Carpenter (1963) observed captive individuals eating their own shed skin and that of conspecifics.

Urosaurus graciosus – Vitt and Ohmart (1975) found shed skin in one of 87 field-collected lizards.

Lacertidae

Heliobolus lugubris – Shed skin was noted in 5 of 45 field-caught specimens (Castanzo and Bauer, 1998).

Lacerta agilis – Gvozdik (1997) found shed skin in a wild-caught lizard.

Pedioplanis lineoocellata – Shed skin was found in one of 43 field-caught specimens (Castanzo and Bauer, 1998).

Pedioplanis namaquensis – Castanzo and Bauer (1998) found shed skin in two of 71 field-caught specimens.

Scincidae

Caledoniscincus austrocaledonicus – Shed skin was found in 3 of 3 field-caught specimens (Bauer and DeVaney, 1987).

Ctenotus grandis – Twigg *et al.* (1996) found shed skin in four stomachs of field-collected specimens (Twigg *et al.,* 1996).

Egernia coventryi – Clemann *et al.* (2004) found shed skin in 26% of 47 wild caught specimens.

Egernia striolata – Bustard (1970) found that four of 35 wild-caught specimens contained shed skin including shed skin from their feet.

Eumeces fasciatus – Fitch (1954) found 23 instances of skink slough in an analysis of 738 food items. McCauley (1939) noted that a half-grown skink had some of its own scales in its stomach. Field (DeGraff and Rudis, 1983)

Eumeces inexpectatus – Hamilton and Pollack (1961) found two of 31 field-collected lizards with shed skin in their stomachs.

Glaphyromorphus emigrans – Skink scales were found in the stomach of one field-caught specimen (Auffenberg, 1980).

Leiolopisma telfarii – Vinson (1975) found pieces of shed skin in the feces of six wild specimens.

Mabuya agilis – Rocha *et al.* (2002) found shed skin in the stomach of a wild-caught specimen.

Mabuya bistriata – Vitt and Blackburn (1991) noted the presence of shed skin in field-collected specimens.

Mabuya frenata – Two of 239 field-collected lizards had shed skin in their stomachs (Vrcibradic and Rocha, 1998).

Niveoscinsus ocellatus – Shed skin was found in stomachs of field-collected specimens (Wapstra and Swain, 1996).

Scincella lateralis – Hamilton and Pollack (1961) noted that one of 142 lizards had eaten shed slough.

Brooks (1964) found that 1% of 327 field-collected specimens contained shed skin.

Sigaloseps deplanchei – Bauer and DeVaney (1987) found shed skin in a single field-caught specimen.

Trachylepis acutilabris – Castanzo and Bauer (1993, 1998) found tail fragments and shed skin in 3 of 146 in field-caught specimens.

Trachylepis binotata – Three of 40 field-caught lizards contained shed skin (Castanzo and Bauer, 1998).

Trachylepis quinquetaeniata – D.G. Broadley (pers. comm.) found shed skin in the stomachs of field-collected specimens.

Trachylepis sulcata – Shed skin was found in 10 of 58 field-caught specimens (Castanzo and Bauer, 1998).

Teiidae

Crocodilurus amazonicus – Captivity (R.E. Honegger, pers. comm.).

Dracaena guianensis – Captivity (R.E. Honegger, pers. comm.).

Varanidae

Varanus niloticus – Captivity (R.E. Honegger, pers. comm.).

Xantusidae

Xantusia henshawi – Brattstrom (1952) found four wild-caught specimens with shed skins in their stomachs.

Xantusia riversiana – Brattstrom (1952) recorded 17 wild-caught specimens from throughout the range with shed skin in their stomachs and Fellers and Drost (1991) found shed skin in 47 of 268 fecal samples and in one of 26 flushed food boluses in wild-caught specimens from Santa Barbara Island.

Serpentes

Pythonidae

Apodora papuana – Captive observation by O'Shea and Bigilae (1991).

Python molurus – Shipkowski (1980) observed a captive male eat pieces of its own shed skin.

Colubridae

Thamnophis sirtalis – Captive observation by Hallman (1998).

Viperidae

Bitis nasicornis – A captive-born juvenile ate a portion of its shed skin (Russell, 1999).

Discussion

The phenomenon of an individual consuming its own shed skin or that of a conspecific has been called keratophagy (Groves and Groves, 1972), epidermophagy (Iverson, 1979), dermatophagy (Weldon *et al.*, 1993), and ceratophagia (Seipp and Henkel, 2000). The use of these various terms, together with a general lack of adequate information in titles, abstracts and key words of articles, has made it difficult to conduct electronic literature searches on this topic. For instance, a recent computer search (using the Institute for Scientific Information [ISI] Web of Knowledge) on the terms "keratophagy" and "dermatophagy," revealed very different results. Only one citation (Kuch, 1998) was common to both searches. Similarly, a pertinent review by Weldon *et al.* (1993) was only revealed by a search on "dermatophagy." Searches on more inclusive phrases, such as "reptiles and diet" or "shed skin in diet" were too vague and either provided mostly irrelevant results or none at all. Use of "reptiles and diet and shed skin" only produced one result, a paper by Vitt *et al.* (2002) which was not included in the results of any of the other searches. We therefore suggest that one common term, keratophagy, be used in reference to an individual with shed skin in its diet. Moreover, abstracts and key words (if applicable) should include this term and phrases with this terminology to maximize the chances of an electronic literature search tagging a given citation.

Some authors have obscured the occurrence of keratophagy in species under study. For example, Pianka (1969, 1986 Appendix E) incorporated lizard sloughed skin in his "lizard and sloughed skin" and "all vertebrate material" categories, respectively, for desert lizards on three continents. It is difficult, if not impossible, to discern which species of the seven in western North America, 19 in the Kalahari Desert of Africa, and 32 in the Australian deserts had eaten their shed skin. Instances of shed skin in reptile diets warrant more detailed attention than it has received previously. Listing number of individuals with observation details would help future reviewers of keratophagy in reptiles better understand the significance of this behavior.

Bustard and Maderson (1965) listed 17 species of lizards that had eaten shed skins, of which four were under natural conditions. Petzold (1982) listed keratophagy in nine genera of geckos, three genera (and two species) of iguanids, and one genus of skink known at that time. Weldon *et al.* (1993) listed 144 species in which keratophagy had been observed in captivity and 16 from literature sources that had occurred in nature. They included two species *(Oedura marmorata, O. tryoni)* listed by Bustard and Maderson (1965) that did not exhibit keratophagy and did not include one that did *(O. monilis)*. We include the corrections in this review. Our list expands the total lizard species known to exhibit keratophagy in captivity to 159 and those in which it has been documented in the field to 89. Undoubtedly, these totals are likely below actual numbers due to the problems with searching the literature on this topic and because many authors have not included specific information on consumption of shed skin in diet studies.

Keratophagy is now known to occur in 16 of the 21 families of lizards recognized by Zug *et al.* (2001) and Hans *et al.* (2004). Of these, Gekkonidae and Iguanidae contain the majority of known instances, 68 and 79, respectively. Twenty-four species of skinks, 18 species of agamids, and ten or fewer species in the remaining families have been documented to exhibit keratophagy. Weldon *et al.* (1993) suggested that most geckos eat their shed skin, however, Bustard and Maderson (1965) noted that at least three species they studied did not. Keratophagy is commonly practiced in some species. *Anolis carolinensis* (Iguanidae) performs this behavior on a regular basis (Bustard and Maderson, 1965). Both juvenile and adult *Eublepharis macularius* (Gekkonidae) eat their entire sheds regularly, if not always. Of 287 observations in captivity, 98% consumed their shed skins (J.D. Groves, pers. obs.). Why do some species eat their skin regularly and others rarely, if at all? This aspect of lizard behavior is obviously understudied.

Nineteen snake species have been observed to consume their own shed skin; all but one of the reported cases of keratophagy are based on captive animals. The only natural observation is of a *Clelia clelia* in Guiana (Beebe, 1946). This behavior is now reported to occur, in addition to the four species noted above, in *Ahaetulla ahaetulla, Alsophis elegans, Bitis arietans, Boiga blandingii, Bungarus fasciatus, Bungarus multicinctus, Clelia clelia, Coluber constrictor, Lampropeltis getula, Lampropeltis triangulum, Naja melanoleucus, Notechis scutatus, Python sebae, Thamnophis sirtalis,* and *Uromacer oxyrhynchus* (Beebe, 1946; Mattlin, 1946; Groves, 1964; Groves and Groves, 1972; Keown, 1973; Groves and Altimari, 1977; Petzold, 1982, 1983; Haagner, 1991; Weldon *et al.,* 1993; Hallmen, 1998; Kuch, 1998; J.B. Murphy, pers. comm.). Klauber (1956) noted that a few snakes are known to eat their shed skins, presumably from his observations at the San Diego Zoo, but that it does not occur in rattlesnakes. The stimuli for inducing this behavior in captivity are unknown but the result may be an artifact of captive conditions.

In a sample of 36 *Trachemys scripta,* Parmenter (1980) found shed epidermal scutes in the stomachs of seven. Parmenter and Avery (1990) mentioned turtle scutes, pebbles, sand and wood in the diet of this species, suggesting that turtle scutes may be ingested while foraging on the bottom of aquatic habitats. This view is consistent with the foraging behavior of this species reported by Moll and Legler (1971). Thus, keratophagy may not be the correct interpretation of this occurrence. The only other record known to us, *Chelodina longicollis,* was a captive reported to us by J.B. Murphy (pers. comm.). Consumption of the relatively large scutes may not occur frequently, although researchers should pay attention to stomach contents and feces to ascertain its relative occurrence. Epidermal scutes of these reptiles may be secondarily ingested while performing other behaviors, such as grooming algae (Reilly, 1973; Meshaka, 1988) or foraging at the bottom of aquatic habitats.

Neill (1971) mentioned that scales of their own or of conspecifics are sometimes found in alligator *(Alligator mississippiensis)* stomachs. We do not believe, however, that crocodilians exhibit keratophagy. Their skin and shedding practices do not suggest this behavior because scales are shed continuously as small flakes and large plates (Zug *et al.,* 2001). The occurrence of scutes reported by Neill may have been cannibalism, a behavior known for crocodilians (Polis and Myers, 1985; Mitchell, 1986).

Of particular interest in our review are the instances of one individual eating the shed skin of a conspecific. Weldon *et al.* (1993) listed occurrences in 16 species in four families of lizards (Agamidae, Gekkonidae, Iguanidae, Scincidae) and none in snakes. We noted its occurrence in one agamid *(Hydrosaurus amboinensis),* two geckos *(Coleonyx veriagatus, Hemidactylus hai-*

tianus), and four iguanids *(Anolis carolinensis, A. roquet, Cyclura cychlura, Uma notata).* All instances were observed in captivity, although the *U. notata* were in a large field enclosure (Carpenter, 1963). Do lizards perform social grooming? What is the purpose of this behavior and under what circumstances does it occur? Additional, detailed observations of this behavior should be published to help build a database for future analysis.

Several hypotheses have been proposed to explain the occurrence of keratophagy in reptiles. We review these views, add two additional hypotheses, and note which ones are amenable to experimental testing.

Nutritional Hypothesis

Taylor (1963) first hypothesized that consumption of neonatal shed skin was the first meal of a neonate lizard, implying that some nutritional value was obtained from it. Bustard and Maderson (1965) explored the possibility that shed skin was a source of vitamin D that had been produced by the action of sunlight in vertebrate skin. They rejected the hypothesis on the grounds that the many recorded observations of slough eating by nocturnal geckos were counter to the presumed correlation of basking with keratophagy. They also suggested that sloughs may be a source of protein. However, to our knowledge, little is known regarding the nutritional and energetic composition of squamate shed skin. Such an analysis would enhance our understanding of whether keratophagy may be nutritionally advantageous.

The nutritional requirements of the 19 snakes noted above were presumably assumed to be filled by the prey provided in captivity. It is not possible to determine whether the physiological state of the snake was deficient in a compound that they may have found in their shed skins. The lack of literature records on keratophagy in snakes weakens the application of the nutritional hypothesis to this group.

Skin sensitivity hypothesis

Some lizards may find the drying slough on their skin irritating and the process of removing it with their mouths triggers an ingestion response. The skin of geckos may be more sensitive than other lizard groups, hence the widespread occurrence of keratophagy in this family. Loveridge (1947) stated that "*T [arentola]. A. annularis* assists the moulting of its extremities by seizing a flake of scarf skin in its jaws and, while holding its claws curled, slowly draws off the slough as if it were a glove. So slowly and carefully is this done that it would seem that the reptile was sensitive about its removal." The skin sensitivity hypothesis seems inappropriate for snakes because the slough had not been removed from the snake's body before consumption in any of the 19 cases noted above.

Artificial Behavior Hypothesis in Snakes

Groves and Groves (1972) concluded that keratophagy in snakes was artificial and possibly influenced by the reptile-eating tendency of these species. Of the 19 species noted above, all but three, *Bitis arietans, Python molurus,* and *Thamnophis sirtalis* are known to include reptiles in their diet. All cases involved captive individuals and, as far as we are aware, none of the snakes repeated the behavior. Although numerous snakes have exhibited cannibalism (Polis and Myers, 1985; Mitchell, 1986), none of those reports or other studies of snake diets (e.g., Uhler *et al.,* 1939; Fitch, 1949, 1999; Ernst and Ernst, 2003) indicated that shed skin had been found in stomachs of wild-caught animals. Thus, the circumstantial evidence supports the artificial behavior hypothesis.

Accidental Hypothesis

Keratophagy may occur because pieces of the skin become entangled in the reptile's teeth and the best means of removal is ingestion (Bustard and Maderson, 1965). These authors' initial observations, those of Weldon *et al.* (1993), and our review of additional species and the literature do not support this hypothesis.

Predator Avoidance Hypothesis

Because predatory snakes and lizards use integumentary-derived, olfactory cues to track their prey (e.g., Weldon and Schell, 1984; Mullin *et al.,* 2004), keratophagy may be a means by which reptilian prey minimize or eliminate some of the cues to which their predators respond. Some lizards, particularly the eublepharine geckos, regularly eat their entire skins. At least some of these lizards (e.g., *Coleonyx variegatus, Eublepharis macularius* and *Hemitheconyx caudicinctus*) also deposit their feces in areas away from their

colonies. In captivity, these communal defecatoriums are generally as far away from the rocks or other cover in their enclosures (J.D.Groves, *pers. obs.*). It is possible that keratophagy in these lizards may serve an antipredator behavior. By placing slough skins in their feces (J.D. Groves, *pers. obs.*) and depositing this material as far away as is possible from where they spend the day, they may deter predatory snakes from finding their locations. Additional work being conducted by one of us (JDG) may shed some light on the relationship.

Some lizards of the Family Agamidae are also known to exhibit feces displacement (Pianka and Pianka, 1970). The North American skink *Eumeces laticeps* can detect chemical odors from sympatric predator snakes and discriminate these chemical stimuli from similar ones derived from a sympatric snake that does not eat lizards (Cooper, 1990). Dial (1990) showed that *Coleonyx variegatus* can also distinguish chemically between predator and non-predatory snakes. Of these lizards, only *C. variegatus,* is known to exhibit keratophagy, however.

Cannibalism can occur in captive snakes if prey odors are detected on a conspecific (Mitchell, 1986). Perhaps keratophagy occurred in some of the 19 snakes above because the shed skin contained prey odors that stimulated prey consumption behavior. Snake skin chemicals serve to stimulate feeding behavior in some species (Weldon and Schell, 1984). They are also detected by lizards, salamanders, and mice so that these potential prey may avoid predation (Madison *et al.,* 1999; Shapley, 2003; Punzo, 2005). We hypothesize that, in some cases, keratophagy may be triggered by chemical cues contained in the shed skin of prospective prey and may therefore be a prelude to a predatory event. If this hypothesis is accurate, one would predict that keratophagy would be more frequent in ophiophagic and saurophagic snake predators, including those that engage in cannibalism (Polis and Myers, 1985; Mitchell, 1986).

Reduced Parasite Load Hypothesis

Reptiles are commonly infested with a variety of ectoparasites, including mites and ticks in terrestrial lizards and snakes (e.g., Chaivabutr and Lawan, 2002; Ameh, 2005). Some reptiles have specialized adaptations that reduce ectoparasite loads. For instance, some species of marine turtles have cleaning symbioses with fishes that remove ectoparasites (Losey *et al.,* 1994; S. H. Smith, 1988). Moreover, many species of lizards have evolved "mite pockets," which typically house damaging chigger mites and presumably limit damage caused by ectoparasites (Arnold, 1986; Bertrand and David, 2004; Salvador *et al.,* 1999; but see Bauer *et al.,* 1990).

The shedding of skin in reptiles, along with the molting of feathers in birds and of hair in mammals, may be a more generalized means of reducing infestations of ectoparasites (Moyer *et al.,* 2002 and references therein). A logical extension of this hypothesis for reptiles is that consumption of the shed skin permanently removes ectoparasites from an individual's habitat, thus minimizing the potential for reinfestation. To our knowledge, there have been no experimental tests of whether skin shedding reduces ectoparasite loads in reptiles. We know of no studies of whether keratophagy minimizes reinfestation of individuals from eggs, larvae and adult ectoparasites contained within shed skins. One prediction of this hypothesis is that individuals with heavier ectoparasite loads should engage in keratophagy more than individuals with lighter loads. Experimentally increasing the ectoparasite load of test individuals and monitoring their keratophagous behavior relative to control individuals could test this prediction. We assume that the parasites are shed with the skin. Although this may be true in some instances, trombiculid mite larvae have their stylets embedded in the dermis and typically are not shed with the skin (A.M. Bauer, pers. comm.). Their bodies might be ripped off from the heads if the shed is pulled appropriately. Thus, extreme care must be taken to ascertain the numbers that are removed and those that remain in whole or in part.

Summary and Conclusions

The results of our review of keratophagy in reptiles suggest that there may be ecological, nutritional, survival, and evolutionary fitness benefits to this behavior, at least for lizards. A more complete understanding of this behavior awaits additional reports and experimental testing of the hypotheses we noted above. Future reports of keratophagy should include a description of the environment in which the reptile performed the behavior, age, size, and sex of the individuals, a complete description of the behavior, and insofar as possible, the individual's nutritional status and prey consumption history. Publication of additional observations in the field and in captivity using standardized terminology is clearly warranted.

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