

SEED DISPERSAL AND PLANT REGENERATION BY SNAKES?

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Abstract. Snakes are known for rare active or passive diaspore ingestion and for very effective digestion. In this study several African snake species were examined for their synecological role as digestive seed predators or seed dispersers. To test digestibility of seeds by snakes, diaspores of several plant species were inserted in dead prey and fed to snakes. All diaspores physically survived the gut-passage through the snakes. Defecation rates and gut-passage times for snakes varied considerably. In comparative germination tests, seeds which had passed through a Spitting Cobra (*Naja nigricollis*) had comparatively low germination rates. Seeds of *Diospyros consolidae* taken from wild bushbaby (*Otelonur garnettii*) faeces had a significantly higher germination rate than seeds which had in addition passed through the cobra, or were taken directly from fruits. In addition, after passing through a Rock Python (*Python sebae*), very hard-coated seeds are also known to have germinated. Possible effects on plant regeneration due to snakes and their prey is discussed for the biocoenosis of the species-rich tropical forest ecosystem of the Shimba Hills (Kenya). Snakes can reduce the risk of pre- and post-dispersal seed predation by feeding on seed-predating rodents in particular. Larger snakes probably contribute to secondary seed dispersal by preying on a wide variety of seed-containing prey. Long gut-passage times of seeds through snakes might, on the one hand, reduce seed viability, but on the other, protect abundant seeds from high seed predation just before rain is available for germination. For hard-coated and 'simple seeds' in particular, secondary seed dispersal by snakes can protect seeds from predation (by preying on seed predators carrying still viable seeds internally), and might help to break up fixed dispersal patterns often caused by rodents like squirrels or rats, forest ruminants and viverrids. Accepted 27 May 1997.

Key words: Snakes, secondary seed dispersal, rodents, post-dispersal seed predation, frugivory, germination tests, *Diospyros*, *Tabernaemontana*, bushbaby, tropical forest regeneration.

INTRODUCTION

Many vertebrate and invertebrate taxa have representatives involved in seed dispersal (= diaspore movement) and/or seed predation. Among the reptiles and amphibians, tortoises and turtles (e.g., Rick & Bowmann 1961, Hnatiuk 1978, Branch 1988, Milton 1992, Mandujano *et al.* 1994; for turtles see Moll & Jansen 1995), some lizards (e.g., Hedges 1983, Iverson 1985, Branch 1988, Fialho 1990, Schall & Ressel 1991, Eugenio & Figueira 1994, Valido & Nogales 1994) and even a frog (Silva *et al.* 1989, Fialho 1990) are known for frugivory and seed dispersal (for review of saurochory, see also Moll & Jansen 1995). However, the extent to which snakes participate in primary or secondary seed dispersal, or seed predation, is poorly known.

A few rare reports indicate active fruit consumption by snakes. According to Mookerjee (1946), an Asian Tiger Python (*Python molurus*) was actually observed swallowing a mango fruit under a tree (*Mangifera indica*, Anacardiaceae), and four more intact fruits with the snake's teeth marks in the pericarp, all infested by two or three insect larvae,

were found in the python's esophagus. Seeds of (c.f.) *Momordica foetida* (Cucurbitaceae), locally also known as "snake food", were found in a "snake's stomach", and frugivory by snakes was also noted for *Capparis tomentosa*, *C. corymbosa* (Capparaceae; Irvine 1953) and for *Vitex micrantha* (Verbenaceae; after Dalziel 1937, from Irvine 1953), among others (for tomatoes, see Rose 1955). Fruit eating by snakes could be triggered by infestation of the fruit pulp by insect larvae (Mookerjee 1946, Pope 1961), by thirst (Rose 1955), or by an attractive odor (Rose 1955), similar to that of prey, which could also have left a smell on the fruit by chance contact (Pope 1961). In the past, fruit consumption by snakes was considered to occur far more often than suspected (Rose 1955; see also Irvine 1953), but it is still "a problem that vexes many herpetologists whether snakes eat fruits and berries" (Pope 1961). Nevertheless, for Pope (1961), a few of the accounts of direct consumption of fruit were beyond doubt, and whether snakes feed on fruit directly or not (see also Isemonger 1968) they still can consume fruits and seeds as secondary food via their frugivorous or granivorous prey (Rose 1955, Pope 1961). As "the digestive juices of snakes are

some of the most powerful chemicals in the world, being able to dissolve the hardest shells and animal bones" (Skinner 1973), "an experimental approach might be used, and it would be helpful to know what ophidian digestive juices make out of such [fruit] food" (Pope 1961). Animals can act as both seed dispersers and ('digestive') seed predators (e.g., Janzen 1971, 1981a, b). Are snakes themselves (secondary) seed dispersers or seed predators by digestion?

This study investigates whether plant seeds will physically survive snake digestion and remain viable, to what extent snakes can contribute to secondary seed dispersal by preying on diaspore-containing prey including seed predators, and how else snakes might prevent seed predation or contribute to plant regeneration.

MATERIALS AND METHODS

To investigate digestibility of seeds, gut-passage times, and seed viability, indirect feeding experiments with snakes (A, B), and subsequent comparative germination tests were carried out (B).

(A) To test general digestibility of seeds by snakes and gain information about gut-passages times, in December 1993 a first series of feeding experiments was carried out at the Snake and Crocodile Farm (Malindi, Kenya) with a number of comparatively hard-coated seeds (some given in their soft-covered fruits) of five different plant species (seed length ranged from 2 to 9 mm, fruit diameter 0.5 to 1 cm; for details see results). A Red-beaked Snake (*Rhamphiophis rubropunctatus*, 1.1 m) and a Rufous-beaked Snake (*Rhamphiophis oxyrhynchus* ssp., 1.0 m), two Red Spitting Cobras (*Naja mossambica*, 1.3 and 1.1 m) and one Puff Adder (*Bitis arietans*, 1 m) were each fed with one dead albino rat (*Rattus norvegicus*) filled with known numbers of diaspores. For a period of 71 hours after feeding, the gut-passage time of diaspores and their physical condition in the faeces was recorded at intervals of less than two hours (during daytime only).

(B) After further feeding experiments at the Bioken Snake Farm (Watanu), viability of seeds was tested in subsequent germination tests. In August 1995, one Black Forest Cobra (*N. melanoleuca*, 1.3 m) was fed with dead domestic chicks filled with 50 fresh seeds of *Bridelia micrantha* (Euphorbiaceae, 4 x 7 mm). In November 1995, a Spitting Cobra (*N. nigricollis* ssp., 1.5 m) was fed with two dead young chicks containing a total of 10 fresh seeds of *Taber-*

naemontana elegans (Apocynaceae, soft seeds, 9 x 12 mm) taken from fresh fruit grown at the snake farm, and 60 seeds of *Diospyros consolatae* (Ebenaceae, hard seeds, 6 x 10 mm). The *Diospyros* seeds given to the snake were collected from several mixed fresh 'wild' Greater Bushbaby (*Otelemur garnettii*) faeces and not directly from fruit, thus these seeds had already been treated by a seed disperser, similar to the seeds snakes find in their natural prey. For comparison, a further 50 seeds from the same mixture of bushbaby faeces were also planted, while seeds for the untreated control were collected on the same morning from fruits of the tree over the bushbaby droppings. After feeding, snake faeces were kindly collected by S. & J. Ashe. In September and December 1995, seeds of all three plant species from both snakes were planted within four weeks after feeding. Handling of seeds was almost identical (including transport to and/or from the snake park). Apart from the seeds of *D. consolatae*, all other untreated seeds used for control and feeding came from the same plant source and were mixed prior to feeding. Germination tests were carried out at an extensive plant nursery at Kwale (coastal Kenya) in boxes filled with local soil. They were protected from rain and direct sun and were kindly watered and checked by J. Muli (and/or the author).

Feeding and defecation frequencies. In addition to seed passage times obtained from own diaspore feeding experiments (A, B), further regular snake feeding and defecation records (as usually noted at the Bamburi Nature Trail) were analyzed in May 1995 for three previous months for two African Rock Pythons (*Python sebae*, 2.3 and 1.8 m), two Puff Adders (mature, length not recorded), one Black Mamba (*Dendroaspis polylepis*, 2.7 m) and one Black Forest Cobra (1.5 m) – though the regular food consists of rats and chicks without diaspores. The feeding scheme was irregular, as is usual for snakes, and modified by the snake park staff according to the size and condition of the individual snakes and the availability of different foods (extracts from their records were kindly provided by P. Mbisi and J. Kahindi, Tony, and Dr. R. Haller).

General remarks. 'Prey' was filled with diaspores through the mouth and anus. All size measurements given are approximate figures. Depending on their availability, apart from *T. elegans*, diaspores were taken from the species-rich Shimba Hills National Reserve (20 km south west of Mombasa, coastal Kenya; for details of the area see Engel 1992). Feeding was

limited by the condition and size of the snakes, their 'prey', and the diaspores, among other factors. Chi² and Fisher's exact statistical tests from the SPSS/PC program were used to test for significant differences in germination. Authority of "pers. unpubl. data" is based on many personal experiments and several years of intensive field studies in the Shimba Hills.

RESULTS

Apart from the Red- and the Rufous-beaked Snakes, the snakes swallowed their prey head first, and no diaspores, even those which were comparatively loose in the mouth or anus of the dead prey, escaped swallowing. As usual, according to the snake parks staff, prey containing the seeds was completely digested with the exception of keratin structures (e.g., hairs, feathers). All hard and soft-covered diaspores appearing in the snake droppings were physically still intact, the seed coatings showing no signs of digestion. For some fruits (see legend of Table 1) the soft exo- and mesocarp appeared separated from the hard-coated seeds.

Germination tests. After passing through the digestive system of the Spitting Cobra (B), seeds of two different plant species, *D. consolatae* and *T. elegans*, were still viable and germinated – though the speed of germination and the germination rate was reduced. The comparatively hard-coated seeds of *D. consolatae* (Fig. 1), taken from bushbaby faeces and later passed indirectly through a Spitting Cobra ('bushbaby + cobra'), had a significantly lower germination rate than those taken from bushbaby faeces only (Chi², $P < 0.001$), or seeds taken directly from fruits (Chi², $P < 0.001$). Seeds from bushbaby faeces had the significantly highest germination rate and also germinated better than seeds taken directly from fruits

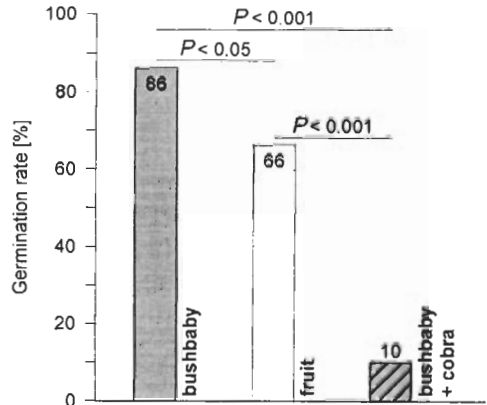


FIG. 1. Proportion of germinated *Diospyros consolatae* seeds taken from wild bushbaby faeces, directly from fruit, and from faeces of a Spitting Cobra (previously fed with chicks filled with seeds from wild bushbaby faeces; $n = 50$ seeds each; for details see text).

(Chi², $P < 0.05$). In addition, one out of nine soft-coated *T. elegans* seeds (= 11%) from the snake faeces, and four out of nine seeds (44%) taken directly from the fruit germinated as well, but no significant effect on germination could be determined for the few available seeds (Fisher's exact test [two tail]: $P =$ not significant). However, after 17 weeks, four (44%) of the soft-coated *T. elegans* seeds from the cobra's faeces still remained intact in the soil while the rest of the untreated control seeds were already rotten. Unfortunately the seeds of *B. micrantha*, both from faeces of the Black Forest Cobra and direct from fruits, rotted in the germination trays.

Gut-passage time. The time from feeding until seeds appeared in the faeces ranged from less than two days

TABLE 1. Proportion of defecated diaspores [% after 71 h] and time until the first faeces with seeds appeared after snakes were fed with seed (s) - and fruit - containing dead rats. All diaspores were physically intact; (Tasi = *Toddalia asiatica*, Rutaceae; Fvi = *Flueggia* (= *Securinega*) *virosa*, Euphorbiaceae; Apav = *Adenanthera pavonina*, Mimosaceae (s); Pdul = *Phitheclobium dulce*, Mimosaceae (s); Bmic = *Bridelia micrantha*, Euphorbiaceae; further see text).

Snake species	Tasi	Fvir	Apav	Pdul	Bmic	time [h]
<i>R. rubropunctatus</i>	100%	50%	100%	100%	100%	40
<i>R. axyrhynchus</i>	1 seed	–	–	–	–	64
<i>N. mossambica</i>	50%	75%	50%	–	100%	<71
<i>N. mossambica</i>	100%	100%	–	–	–	63
<i>B. arietans</i>	–	–	–	–	–	>71

up to around 10 to 14 days (A, B, and probably more for Puff Adder, A). In less than one hour after feeding, the Rufous-beaked Snake (A) had regurgitated most of the diaspores, but not the rat. After swallowing the diaspores, all subsequent first droppings already carried seeds, although not all seeds appeared in first droppings (A). The Red-beaked Snake defecated after 40 hours, and, apart from the Puff Adder, all other snake species after less than 71 hours (A, Table 1). After 71 hours some diaspores were still inside the snakes, particularly in the case of the less agile Puff Adder, but intact seeds were defecated later (A; M. Easterbrook, pers. comm.). The seeds of *B. micrantha* (B) occurred intact in the droppings of the Black Forest Cobra after 10 to 14 days (exact duration unknown), seeds of *D. consolatae* and *T. elegans* (B) after less than two weeks (but more than two days, exact duration unknown; Spitting Cobra).

Average time between two defecations. As analyzed from the permanent records of the Bamburi Nature Trail, the time between two defecations varied considerably, ranging from 6 to 29 days (for details see Table 2). Apparently, and even for the similar cobra species, the other tested snake species from Malindi (A; Table 1) defecated much faster than the tested (C, Watamu) and the 'non-tested' snakes from the Bamburi records (Table 2; except perhaps for Puff Adders).

DISCUSSION

Seed ingestion, viability and germination. Apart from the experiments presented in detail here, several more tests were carried out with other plant and snake species. As an additional result, two out of three very hard-coated seeds of *Adenanthera pavonina* (Mimosaceae, introduced, used as a red passage marker),

which passed through an African Rock Python, germinated as well, indicating good seed viability for these hard-coated seeds after passing through a python. However, the seeds of *T. elegans* and *D. consolatae* in the comparative tests had reduced germination rates (compared with the control seeds) after passing through a snake (and previously a bushbaby, Fig. 1), thus, in these tests, neither secondary seed dispersal nor gut-passage by snakes improved seed germination. Nevertheless, despite the low germination rates in these single and unreplicated tests with snakes, seeds of *B. micrantha* (among others in unpublished tests), which failed to germinate, though not necessarily due to the passage through snakes, were still physically intact and probably viable after passing through snake digestive systems. In general, improvement in germination rates of seeds due to 'passing through an animal gut' seems to be a thesis that is probably overemphasized (see also Witmer 1991). Indirect or mechanical effects, rather than the direct influence of partial chemical digestive reactions on the diaspores, can cause higher germination rates (e.g., killing of seed-predating beetles in the gut, Lamprey *et al.* 1974, or damaging the exocarp or other seed covers). Comparative germination tests, when repeated under slightly different conditions, can even result in opposite germination rates (Engel 1992). Thus, in the field, germination rates of seeds from snake faeces could also be higher. For secondary seed dispersal by snakes, negative synergetic effects on seed viability after treatment by several animals might occur in the field as well as in experiment (e.g., bushbaby and cobra, Fig. 1), but the effect of the more intensive and longer passage through the snake is probably predominant. However, unlike some other seed dispersers, and most

TABLE 2. Mean length and range of time between two defecations [days] of several snakes. Feeding and defecation of regular food without diaspores. Analysis of Snake farm records for three months.

Snake taxa	Number of feedings	Number of defecations	Mean length of time [\pm SD] between two defecations	Range of time between two defecations
<i>P. sebae</i>	9	3	27.5 \pm 2.1	26–29
<i>P. sebae</i>	7	5	18.0 \pm 5.6	13–26
<i>B. arietans</i>	7	7	12.0 \pm 9.3	7–13
<i>B. arietans</i>	5	7	10.5 \pm 3.9	7–17
<i>D. polylepsis</i>	9	8	10.5 \pm 4.3	6–18
<i>N. melanoleuca</i>	10	8	10.7 \pm 4.5	6–17

seed predators, snakes cannot destroy seeds selectively or accidentally by chewing or gnawing with their teeth. Usually, controlled germination tests are carried out and calculated with seeds remaining intact in the faeces, but the often high number of seeds which, for certain species combinations, are already incapable of germination because of chewing (selective: e.g., *Lantana* seeds and baboons; non-selective: elephants, pers. unpubl. data) remain unconsidered for the calculation of germination rates. If success of seed germination were to be measured in terms of the total number of seeds handled by a 'disperser' (including seeds destroyed in the mouth), snakes could show a comparatively improved germination balance.

Besides typical endozoochory with possible effects on seed viability, regurgitation by snakes occurs occasionally (S. & J. Ashe, pers. comm.; pers. observation). Snakes "can disgorge at will prey partly or wholly swallowed, or partially digested" (Pitman 1974). If the milieu of snake guts reduces seed viability, regurgitated seeds can contribute to the seed bank without being affected by a complete passage through a snake. In addition, particularly after swallowing big prey, snakes are more vulnerable (for python: Branch 1988), and 'superpredation' on seed-containing snakes by further carnivorous predators (e.g., Irvine 1954, Isemonger 1968, Easterbrook 1972, Skinner 1973, Pitman 1974, Haltenorth & Diller 1977, Branch 1988, Dorst & Dandelot 1990, Skinner & Smithers 1990, Marais 1992) can also reduce the exposure time of seeds in snakes.

Synecological context. The possible role of snakes in plant regeneration should be taken into account in areas where snakes, granivores and/or frugivores are common, which is the situation in most intact tropical (forest) habitats. As discussed below for the Shimba Hills, seeds which are actually carried inside the mouth or gut of potential snake victims could gain additional dispersal in time and space, but snakes could also reduce the risk of pre- and post-dispersal seed predation.

Gut-passage times and seed dispersal. In addition to the findings of the experiments presented here, the comparatively soft-coated seeds of *Tabernaemontana pachysiphon* (Apocynaceae), and some hard-coated seeds, appeared physically undamaged in the first or second droppings of three African Rock Pythons after seven, eight, and more than 20 days; for Puff Adders, after 15 and 16 days in the first faeces after feeding

(pers. unpubl. data). After feeding, diaspores did not always occur in the next defecation (Table 1), thus the maximum range of 29 days between two defecations (compare Table 2) could even be extended for another interval in respect of diaspore throughput. According to the size of the meal, digestion might be fairly protracted (though faster than mentioned here, compare Pitman 1974). For snakes in captivity, information on gut-passage times and speed of digestion or new food intake varies considerably from some several hours (e.g., Black Mamba, Easterbrook 1972) to several years (many reports by Pope 1961; for python see also Cansdale 1965, Skinner 1973, Marais 1992). Long gut-passages, or highly delayed defecation for a minority of individual diaspores, are also known from other 'frugivores' (e.g., Rick & Bowmann 1961, Janzen 1981a,b), but, generally, for most other seed dispersers including other reptiles, feeding and defecation frequencies (per day) are much higher and the gut-passage times usually shorter, ranging from minutes to a few days (e.g., Sikes 1971, Charles-Dominique 1978, Engel 1992, pers. unpublished data for several seed dispersers). However, depending on their need for shedding, hibernation, etc., snakes and their gut-passage times are highly variable and their life seems basically cyclic (Pope 1961). Nevertheless, in an environment full of danger for snakes (see 'superpredation'), long gut-passage times, combined with avoidance, escape and other regular movement reactions, can result in some uphill dispersal, in particular by large and agile snake species (i.e., cobras, mambas) and African Rock Python (up to 50 meters uphill, and likely much more, were observed by locals and the author for several species). The need of food and water can cause directed snake wanderings of up to two miles from base (Pitman 1974). Slow locomotion in some snake species could be compensated for by comparatively long passage times (e.g., Puff Adder, see Table 2). However, long gut-passage times might increase the risk of digestive seed predation, since non-dormant and soft-coated seeds in particular might start to germinate in the gut, a mechanism (quiescence) that might work in elephants (few pers. observations) or after rain, but unlikely in the digestive juices of snakes. On the other hand, visible signs of germination or digestion were not observed for any seed which had passed through a snake (though it might have started inside some seeds). In the Shimba Hills, many seeds out of around 1100 known plant species are dormant or hard-coated and quiescent (pers.

unpubl. data) and are therefore comparatively resistant to digestion, and, as discussed below, long gut-passage times could be advantageous in other respects.

Snakes saving seeds from seed predation? The comparatively long gut-passage times of larger snake species could also be a temporal mechanism, reducing common post-dispersal seed predation (compare, e.g., Janzen 1971). In the Shimba Hills, the end of the dry season seems also to be a main fruiting season for many plants (Q. Luke, pers. comm.; pers. unpubl. data), thus (secondary) seed ingestion by snakes becomes more likely just weeks before the rains start. During this critical period of pre- and post-dispersal seed predation (compare e.g., Janzen 1971, Vander Wall 1990), diaspore ingestion and delayed seed defecation by seed-carrying snakes can reduce the risky post-dispersal exposure time for seeds. Since seeds are inside snakes, snakes might act as 'temporary safe sites', preventing seeds from typical seed predation by mainly insects and rodents. In addition, the non-soluble faecal material (and often hairs), where seeds are usually embedded, might act as an additional long-term protection (repellent) against post-dispersal seed predators. For comparison, seeds at African Civet (*Civettictis civetta*) latrine sites embedded in prey hairs seemed less predated than unprotected seeds, and Giant Rats (*Cricetomys gambianus*) preferred exposed seeds rather than hidden ones (pers. observ.). However, in the field, decomposition of most frugivore faeces can vary considerably (pers. observations), and though it seems unknown to which extent snake faeces will be affected or worked into the soil, during the rainy season most seeds will absorb moisture and start germinating even in the protective faeces or remaining hairs, though soil might be a better safe site against occasional drought.

Snakes and seed distribution. Feeding on seed-containing prey by snakes can also result in inhibiting unidirectional dispersal, and, consequently, altered seed distribution patterns; i.e., secondary dispersed seeds can reach new sites, and can escape from dense accumulations with probably enhanced competition and seed predation (compare, e.g., Janzen 1970, Howe 1989) at feeding and latrine sites, (Engel 1992, for viverrids), hoarding (Vander Wall 1990, for rodents) or resting sites (Feer 1995, for forest ruminants).

Interacting species. In the Shimba Hills, as in most other African forest areas, rodents like Giant Rats and squirrels, among many other seed predators and seed dispersers, are potential prey of many snake species (see Table 3; S. & J. Ashe, pers. comm.; for antelopes, other large or unexpected prey and more details see also, e.g., Pope 1961, Cansdale 1965, Isemonger 1968, Skinner 1973, Branch 1988, Marais 1992). Seed predators, being mainly destructive for diaspores, can still carry viable seeds in their mouth or cheek pouches (i.e., Giant Rats almost always carried intact seeds only, pers. unpubl. data) or, exceptionally, even in their guts (e.g., Janzen 1971, pers. unpubl. data for Giant Rat, porcupine, suni, duiker). Snakes are known to control rodent populations and were even used very effectively for 'pest control' (i.e., to reduce numbers of rats, Skinner 1973) and protected by law (in Zimbabwe, *P. sebae* was for this reason included in the "Royal Game list", Isemonger 1968). Feeding on rodents in particular by snakes could have several positive consequences for regeneration of plants: (1) preying on rodents will lower total pre- and post-dispersal seed predation by rodents, (2) where hoarding occurs, snakes can save hoarded diaspores from later predation, e.g., by feeding on squirrels, (3) snakes can save carried seeds from later predation, e.g., by feeding on seed-carrying Giant Rats (which will usually hoard seeds only briefly and/or too deeply for regeneration, Skinner & Smithers 1990, Engel 1992). Apart from granivorous rodents, frugivorous, but otherwise mainly seed-predating antelopes (pers. unpubl. data of feeding experiments for small, hard or soft seeds) can still act as seed dispersers after being killed, as long as during rumination at least some small diaspores are not destroyed (S. Baer, pers. comm.; compare also Dubost 1984, Feer 1995, but see the latter also for 'spit dispersal' for large, hard seeds and endozoochory by antelopes). Many African snakes include common granivorous or frugivorous birds in their prey, and pythons even prey on bigger species up to the size of hornbills (J. Ashe, pers. comms.; for 'birds and diaspores' of the Shimba Hills compare also Engel 1992 with Maclean 1988). Puff Adder, Gaboon Viper (*Bitis gabonica*) and Black Mamba might feed on Greater Bushbaby; Black Mamba might also be able to catch frugivorous genet cats (*Genetta* spp.); hedgehog (*Erinaceus albiventris*) spines are often found in wild Puff Adder droppings (S. & J. Ashe, pers. comms.), and Puff Adder diet also includes frugivorous tortoises (Branch 1988). For other areas many other species combinations are possible.

Interactions and activity patterns of snakes and their prey. Depending on their activity patterns, snakes can hunt for active or sleeping nocturnal (or diurnal) prey, and their respective activities might overlap as many animals follow no strict temporal and spatial patterns and many snakes are not strictly arboreal or terrestrial (see for some species, e.g., Isemonger 1968, Skinner 1973, Branch 1988, Marais 1992). In contrast to findings from captivity, in the field, pythons, for example, are assumed to consume at least one rat per day (Skinner 1973) and Puff Adders are even known to consume many rats in a single night (Pitman 1974). In the Shimba Hills, the high numbers of snakes and their frugivorous/granivorous prey almost ensure occasional secondary seed dispersal by snakes.

Conclusions. Considering the need for food of both snakes and their frequent granivorous and frugivorous prey, a possible high turnover in secondary seed dispersal becomes obvious even if few prey contain viable seeds. However, the feeding and defeca-

tion habits of snakes seem highly variable and far from understood in the field. As far as is known, seed dispersal for most plants, in particular for those with fleshy fruits, will not exclusively depend on snakes or any other rare events, and, compared with the frequency of other dispersal mechanisms, (secondary) seed dispersal by snakes seems rather the rare exception than the rule. In addition, the density of small rodents and most frugivores is higher than that of snakes. Warm-blooded seed dispersers are more active and will therefore, while alive, contribute much more on their own or by coincident ('seed predators', see, e.g., Vander Wall 1990). Nevertheless, mortalities of either transporting or hoarding seed predators caused by snakes or other (accidental) causes might, in addition to ordinary dispersal systems, help to explain how plants, particularly those with hard-coated 'simple seeds' (see Janzen 1984, Dean & Milton 1988) consumed by seed predators, manage to disperse seeds against gravity (barochory, hydrochory) or some other directed dispersal. Over thousands of

TABLE 3. Some snake species of the Shimba Hills and their potential frugivorous or granivorous prey (xx: very likely, x: likely, r: rare, -: not possible, remainder unknown).

Snake species	Mainly seed predators										?			
	Rodents					Ruminants					Others			
	<i>Cricetomys gambianus</i>	<i>Hystrix</i> spec.	<i>Panaxerus ochraceus</i>	<i>Panaxerus palliatus</i>	<i>Heliosciurus</i> spec. other rodents	<i>Neoragrus moschatus</i>	<i>Sylvicapra gymmias</i>	<i>Cephalophus monticola</i>	<i>Cephalophus natalensis</i>	<i>Tragelaphus scriptus</i>	primates	other mammals	birds	reptiles (incl. snakes)
<i>Python sebae</i>	xx	x	x	x	x	xx	x	x	x	x	x	x	x	r
<i>Dendroaspis polylepis</i>	xx	-	x	x	x	xx	-	-	-	-	x	x	x	r
<i>Bitis arietans</i>	xx	-	x	x	x	xx	-	-	-	-	x	x		x
<i>Bitis gabonica</i>	xx	-	x	x	x	xx	-	-	-	-	x	x		
<i>Dendroaspis angusticeps</i>						x	-	-	-	-				xx
<i>Naja mossambica</i>	xx	-				xx	-	-	-	-	x	x	x	x
<i>Naja melanoleuca</i> ^{1,2}	xx	-				xx	-	-	-	-	x	x	x	x
<i>Rhamphiophis rubropunctatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	x
<i>Dispholidus typus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	xx
<i>Thelotornis kirtlandii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	xx
<i>Telescopus semiamulatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	x
<i>Telescopus dhara</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	x
sand snakes ^{2,3}	-	-	-	-	-	-	-	-	-	-	-	-	-	x

¹Note: the Egyptian Cobra, *Naja haje annulifera*, might occur as well, ²*Psammophis punctulatus* and/or *P. sibilans* and/or *P. subaenariensis*; ³presence unclear; all other species recorded or collected by the author (incl. seven smaller non-listed species).

years, all types of dispersal modes might contribute to plant regeneration and help to self-maintain (tropical) biocoenoses, and even rare or stochastic events might cause high impact (see, e.g., Levey & Byrne 1992, Cramer 1993). As a matter of fact, and despite low germination rates in only two successful comparative tests indicating a strong tendency towards 'digestive seed predation' by snakes, viability of seeds was nevertheless proved for three plant species by germination after passing through the digestive system of a cobra or python (where two out of three very hard-coated seeds germinated), thus proving that snakes can contribute to plant regeneration. As long as the "ecology of African snakes" remains a "major gap in our knowledge" (Shine *et al.* 1996) and detailed investigations of (secondary) seed dispersal by snakes under natural circumstances remain a challenge for modern field herpetology, snakes should be taken into account as occasional, 'unpredictable, complex seed predators, seed savers and even seed dispersers'. Irvine's (1953) considerations on primary frugivory by snakes might be explained by snakes waiting to prey on frugivores or granivores at fruiting plants (see also Isemonger 1968), and this could also explain how he found *Momordica* seeds in a "snake's stomach" after the seed-containing prey had been already digested (see also Rose 1955). However, 36 years after Pope's (1961) suggestion, it has been proved that (a few) seeds can survive a snake's digestion in a still viable condition. As discussed for other reptiles (and even a frog, see introduction), it would be more interesting to find out in the field whether snakes might play any important role in the regeneration of plants.

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