Intrinsic and Extrinsic Factors Influence Expression of Defensive Behavior in Plains Hog-Nosed Snakes (*Heterodon nasicus*)

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Abstract

Animals failing to deter predation are eaten. Among the many deterrents to predation, antipredator behaviors are perhaps the most variable, ranging from active (fight or flight) to passive (immobility). We assessed variation in the expression of a passive defensive behavior, death-feigning, in Plains Hog-nosed Snakes (*Heterodon nasicus*) and predicted that intrinsic and extrinsic factors would influence the duration of this behavior and the latency to its onset. We simulated predatory attacks on 27 snakes encountered in the field, and analyzed the behavioral responses of snakes as a function of differences among individuals (sex and size) and environmental factors (temperature and microhabitat). Larger snakes death-feigned for longer durations than smaller ones; this relationship was stronger for female snakes than for males. Death feints were initiated sooner when snakes were encountered at higher temperatures. Extrinsic factors had a greater influence on latency to death-feigning behavior, whereas intrinsic factors more strongly influenced its duration. Because our results involved wild snakes, they provide an improved, highly relevant understanding of individual and environmental factors that regulate the expression of immobile defensive behavior. Furthermore, additional hypotheses can now be proposed that address the evolution of defensive behaviors that leave animals prone to attack.

Introduction

Defensive behaviors mediate trophic interactions between prey and their predators. These behaviors vary within a species due to environmental cues, phenotypic plasticity, ontogeny or other mechanisms (Lang et al. 1977; Kalin et al. 1991; Shine et al. 2000). Although behavioral flexibility is required for effective defense, stable strategies can evolve that maximize fitness of individuals with particular traits or in certain situations. Understanding how defensive behaviors are influenced by such factors and interactions among them can help identify the physiological and ecological determinants of these traits.

Antipredator behavior is somewhat flexible because the same prey species might be targeted by several different predators with diverse strategies (Eilam 2005). Prey that can execute versatile, flexible defensive responses should have high overall survival probability. Individual differences among prey can also influence their defensive response, because certain combinations of traits have high fitness. For example, correlational selection between dorsal pattern and antipredator behavior has been linked to survival in northwestern garter snakes (*Thamnophis ordinoides*; Brodie 1992). Furthermore, environmental factors such as temperature can influence defensive behavior (Gomes et al. 2002; Miyatake et al. 2008a), especially among ectotherms. Determining the causes of variation in defensive behavior is critical to evaluating the function of these behaviors and understanding their evolution.

Many animals exhibit an immobility response to threat, instead of an active defense such as fight or flight (Hoagland 1928; Arduino & Gould 1984; Eilam 2005). Because a prey animal cannot freeze and flee simultaneously, these types of defenses are mutually

exclusive. Many species have been shown to exhibit substantial interindividual variation in immobility behaviors, correlated with such factors as hormone levels (Miyatake et al. 2008b), mating history (Kuriwada et al. 2009), diet (Magladery et al. 1979; Mori & Burghardt 2000), genetics (Prohammer & Wade 1981; Nakayama & Miyatake 2009, 2010), social cues (Thompson & Liebreich 1987), and environment (Hennig 1979; Ewell et al. 1981). Immobility behavior has been linked to increased survival in several predator–prey interactions, such as those between ducks and foxes (Sargeant & Eberhardt 1975), quail and cats (Thompson et al. 1981), and beetles and jumping spiders (Miyatake et al. 2004). Many immobile animals continuously monitor their environment (Klemm 1971; Gallup et al. 1980) and can modify the duration of their immobility in response to changes in their opportunity to escape (Hennig et al. 1976; Ewell et al. 1981). Edelaar et al. (2012) reported that measures of tonic immobility were highly repeatable within individual wild birds and suggested that measures of immobility behavior are meaningful traits for studies involving antipredatory behavior in wild populations.

Several snake species exhibit immobility responses when disturbed (Gehlbach 1970; Greene 1988). The best known of these are the North American Hog-nosed Snakes (genus *Heterodon*) which, when disturbed, often exhibit a motionless inverted posture with the mouth open, sometimes accompanied by defecation or vomiting (Platt 1969). Raun (1962) demonstrated that the behavior is innate, and Burghardt & Greene (1989) showed that *Heterodon* uses vision to monitor threats and modifies the duration of the inverted phase accordingly, suggesting that death-feigning in *Heterodon* is not an entirely involuntary reflex. Relatively few studies have investigated immobility behavior in this genus (Edgren & Edgren 1955; Hemken 1974; Durham 1980; Burghardt & Greene 1989; Burghardt 1991). All have used clutches of juvenile snakes and none have been conducted in the wild. We present the first data on the immobility behavior of *Heterodon nasicus* (Plains Hog-nosed Snakes) in the wild and analyze behavioral variation as a function of individual differences in sex, size, and environmental factors. We tested the hypotheses that sexual, ontogenetic, and environmental differences would be present in latency to and duration of immobile defensive behavior in *Heterodon*.

Methods

We collected snakes while walking a 1.85-km transect between 0830 and 1145 h on 22 d between 18 May and 25 Jun. 2010. Typically, four to eight people visually searched for snakes in the complex habitat of open sand, bunch-grasses, and herbaceous plants. The transect was located at the Thomson Sand Prairie, a unit of the Upper Mississippi River National Wildlife & Fish Refuge located in Carroll County, Illinois, along the eastern border of the Mississippi River.

Upon detection of an individual *H. nasicus* by one of the transect walkers, we immediately started recording snake behavior using a Canon G10 digital camera. We recorded the reaction of each snake to standardized harassment, which consisted of tapping the snake approximately twice per second on the head with the fingers to simulate attack by a predator. If a snake inverted its body, tapping was ceased to simulate the putative effect of the behavior on a startled or disinterested predator. If a snake subsequently ceased feigning death, tapping was resumed. Because *H. nasicus* are known to increase the duration of their bodily inversions when exposed to predator eye contact (Burghardt & Greene 1989), the observer kept his gaze on the screen of the camera throughout the duration of filming, so that the snake could be watched without looking directly at it. Each snake was filmed for 120 s. Any trials that were interrupted by unusual circumstances (e.g., interference by other observers) were omitted from the analysis.

Each recording was scored for the number of seconds to body inversion (latency) and subsequent number of seconds to re-righting (duration of inversion). Initiation of death-feigning was taken to be the moment of body inversion. If a snake did not invert its body, it was considered a censored data point in the analysis, because the trial ended before the event of interest. We recorded whether or not each snake defecated during the trial. The sex and size (snout-vent length; SVL) of all snakes were recorded following filming. Because of large natural breaks in the size data for both sexes, we classified snakes into age classes as either juveniles or adults for some analyses, following Kolbe (1999; adult ≥300 mm SVL). Although reproductive status is known to affect defensive behavior in snakes (Brodie 1989), this phenomenon could not be assessed in our study, because all adult female snakes tested were gravid at the time of testing. Microhabitat was categorized as open or vegetated from videos (A. M. Reedy & A. M. Durso, own data). Time stamps extracted from each video allowed us to obtain measurements of temperature taken on an hourly basis by a nearby weather station (National Weather Service Mississippi River Lock and Dam 13). All snakes were marked to avoid repeat sampling and released at their site of capture.

We used time failure (survival) analyses (PROC PHREG in SAS 9.3) of occurrence of inversion (the categorical response variable) and, for snakes that responded by inverting, the duration of, or latency to, inversion (the continuous response variables) to model the behavioral response of snakes to our predator simulation. We investigated differences in behavior as a function of individual differences (sex and size) and differences in environment (microhabitat and temperature), as well as interactions of these four variables. We used a generalized linear model (PROC GLM) to test for relationships between temperature, latency, duration, and size (continuous explanatory variables) and snake defecation (categorical response variable).

The nature and degree of disturbance received during a predator–prey encounter might be more important than the effects of sex, size, microhabitat, and temperature in determining immobility duration (Dodd 1989; Gregory 2008; Mehta & Burghardt 2008). Because available sample size was limited, we did not introduce any treatments to examine the efficacy of predator simulation method, as has been carried out in other studies (Burghardt & Greene 1989; Cooper 1997).

Results

Defensive behavior of 27 snakes was recorded, of which 11 were male and 16 were female. Snakes varied in size from first-year juveniles to mature adults (Table 1). In total, behavior of 11 female and 7 male juvenile snakes and five female and four male adult snakes was recorded. All adult snakes were found in vegetated microhabitats, primarily grass. All but two of the 17 juvenile snakes were in open microhabitats (bare sand). Although temperature varies among microhabitats at our site (A. M. Reedy & A. M. Durso, own data), temporal variation in temperature greatly exceeds spatial variation, and air temperatures at time of testing represented a wide range of overall environmental variation in temperature, from 14 to 26°C ($\bar{x}$ = 19.6°C).

All snakes except one exhibited stationary defensive behavior and made few if any attempts to flee. One adult female snake (SVL = 593 mm) was encountered near the entrance to a hole in the ground and did not exhibit death-feigning behavior, but rather made repeated attempts to reach the hole entrance during the 2-min trial. This outlying point was eventually omitted from the analyses. An additional four snakes remained immobile but never inverted their bodies. These points were not omitted from analyses but were considered censored in the duration analysis and assigned latency equal to the trial time (120 s) in the latency analysis. Overall, when only responding individuals were considered, juvenile snakes death-feigned for shorter durations (23 ± 21 s; standard deviations reported) than adult snakes (72 ± 40 s), although latency to inversion of juveniles (15 ± 15 s) and adults (20 ± 17 s) was similar.

Initially, the model for duration of inversion was not improved by the addition of parameters (sex, size, temperature, microhabitat, and their interactions; ΔAIC < 2), and no model parameters showed significant effects (although several were of marginal significance). When we completed an analysis without the outlying point, the model for duration of inversion was improved by the addition of parameters (Table 2, ΔAIC = 10.6). Alone, the main effect of sex was

Table 1: Morphology of wild *Heterodon nasicus* (n = 27) videotaped from May to Jun. 2010 at Thomson Sand Prairie, Carroll Co., Illinois. Standard errors are reported. Snakes were classified as juvenile (SVL ≤300 mm) or adult (SVL > 300 mm) using natural breaks in the data. Mass of adult snakes was measured with lower precision than mass of juvenile snakes

	n	SVL (mm)	Tail length (mm)	Mass (g)
Juvenile				
Female	11	191 ± 9	26 ± 0.5	7.67 ± 1.1
Male	7	184 ± 5	33 ± 0.5	7.48 ± 0.6
Adults				
Female	5	535 ± 22	77 ± 1	193 ± 22
Male	4	467 ± 32	96 ± 4	108 ± 17

SVL, snout-vent length.

Table 2: Model fit statistics and parameter likelihood estimates for four models of intensity of *Heterodon nasicus* defensive behavioral response

Response variable	Model	AIC	Parameter	χ^2	p-value
Duration	Null	103.2	–	–	–
	Global	92.6	**Sex**	**4.54**	**0.03**
			Size	2.28	0.13
			Microhabitat	0.01	0.99
			Temperature	**3.29**	**0.07**
			Sex*Size	**4.37**	**0.04**
			Sex*Temp	**4.62**	**0.03**
			Sex*Size*Temp	**4.51**	**0.03**
Latency	Null	101.1	–	–	–
	Global	99.5	Sex		NS
			Age class		NS
			Microhabitat		NS
			Temperature	**7.07**	**0.0078**

Parameters having significant or marginal contribution to each model are indicated in bold. Only significant interaction terms are shown.

related to the duration of inversion (females inverted for longer than males, p = 0.03, Fig. 1), whereas the main effect of temperature was of marginal importance (p = 0.07, Fig. 2), and the main effects of size (p = 0.13) and microhabitat (p = 0.99) were not related to death-feigning duration. However, the interaction terms indicate that there is a sex-dependent effect of size (p = 0.04) and temperature (p = 0.03) on death-feigning duration. Specifically, the positive relationship between body size and death-feigning intensity in female snakes was steeper than it was in male snakes (Fig. 1). The three-way interaction among sex, size, and temperature was also significant (p = 0.03).

Duration of inversion was shorter in open microhabitats (19 ± 13 s) than in vegetated microhabitats (62 ± 42 s). Additionally, all snakes in vegetated microhabitats exhibited death-feigning except for the aberrant adult female that was captured near a hole, whereas four of the 14 snakes in open microhabitats did not exhibit death-feigning. However, no model terms incorporating microhabitat were related to duration of inversion (p ≥ 0.99).

When size was included as a continuous covariate in the model for latency to inversion, no effects were significant. Instead, we used the juvenile and adult age class categories to parameterize this model. Temperature was the only important predictor of latency for this model (p = 0.008), wherein snakes exhibited shorter latency to inversion at higher temperatures
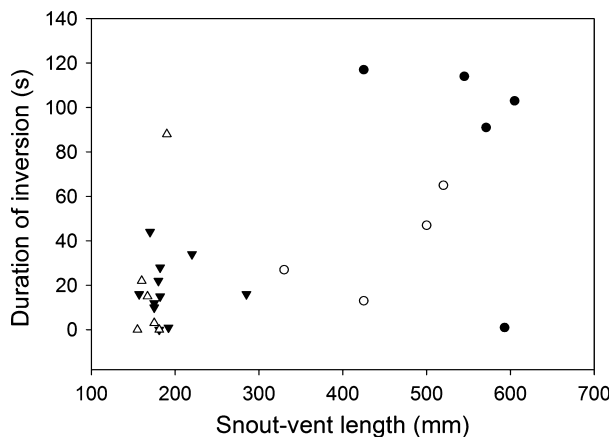
(Fig. 3). Neither model for latency was improved by the addition of parameters (Table 2, ΔAIC < 2).

Temperature and duration of inversion were not related to defecation. Snake body size was marginally important in predicting defecation (p = 0.08). Snakes that defecated had a much shorter latency to
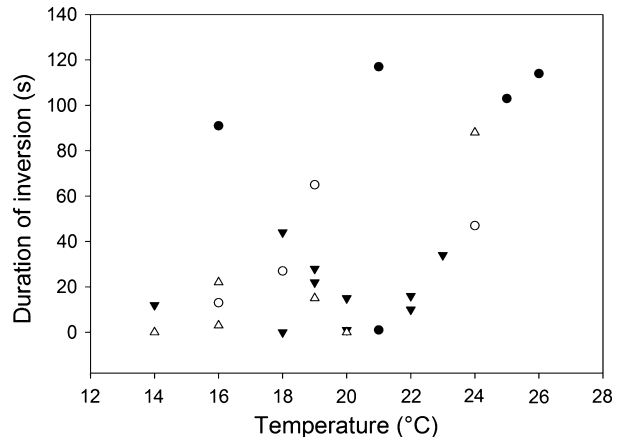

Fig. 2: Effect of temperature on duration of inversion among *Heterodon nasicus* of differing sexes and sizes, observed from May to Jun. 2010 at Thomson Sand Prairie, Carroll Co., Illinois. Hollow symbols represent male snakes, solid symbols represent females. Triangles represent juvenile snakes (SVL ≤ 300 mm), circles represent adult snakes (SVL > 300 mm). A marginally non-significant effect of temperature on duration of inversion was present (p = 0.07). The omitted point is visible in the bottom center – see text. SVL, snout-vent length.
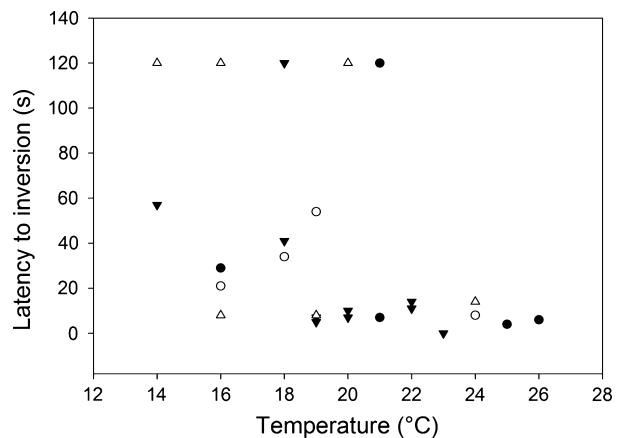

Fig. 1: Effect of individual differences on duration of inversion among *Heterodon nasicus* of differing sexes and sizes, observed from May to Jun. 2010 at Thomson Sand Prairie, Carroll Co., Illinois. Hollow symbols represent male snakes, solid symbols represent females. Triangles represent juvenile snakes (SVL ≤ 300 mm), circles represent adult snakes (SVL > 300 mm). A significant sex*size interaction was present (p = 0.04). The omitted point is visible in the lower right (adult female, SVL = 593 mm) – see text. SVL, snout-vent length.

Fig. 3: Effect of temperature on latency to inversion among *Heterodon nasicus* of differing sexes and sizes, observed from May to Jun. 2010 at Thomson Sand Prairie, Carroll Co., Illinois. Hollow symbols represent male snakes, solid symbols represent females. Triangles represent juvenile snakes (SVL ≤ 300 mm), circles represent adult snakes (SVL > 300 mm). A significant effect of temperature on latency to inversion was present (p < 0.008). Five snakes that did not invert are depicted as having latencies to inversion of 120 s, including the omitted point, visible in the upper right – see text. SVL, snout-vent length.

inversion than snakes that did not (p = 0.03). This relationship held true when body size was included as a covariate (p < 0.005).

Discussion

Quantifying the variation in defensive behaviors expressed by wild animals as it relates to different environmental and individual factors is important to understanding the evolution of those behaviors. We investigated variation in immobile defensive behavior for the first time in a population of wild *Heterodon*, a genus that is widely regarded as having unusual and elaborate defensive behavior. We documented effects of intrinsic (sex, size) and extrinsic (temperature) factors and their interactions on antipredator behavior in wild *H. nasicus*. Extrinsic factors appeared to play a greater role in regulating latency to death-feigning behavior, whereas a combination of intrinsic and extrinsic factors affected the behavior's duration.

To our knowledge, this is the first study to examine sexual differences in antipredator behavior of wild adult snakes (Shine 1993). Our primary result was that adult female *H. nasicus* death-feigned for longer durations than juveniles or adult males. The reproductive status of females almost certainly has an impact on their exposure to predation and defensive behavior (Brodie 1989; Creer 2005), but lack of variation in female reproductive status in our sample precluded explicit investigation of this effect. The three-way interaction among sex, size, and temperature further indicates that their high level of reproductive investment is the cause of the long death feints of adult female snakes, because only adult females exhibited long durations of inversion regardless of the temperature (Fig. 2). Further evidence supporting the idea that reproductive status affects defensive behavior was reported by Burghardt (1991), who observed that the latency to inversion of a captive female Eastern Hog-nosed Snake (*Heterodon platirhinos*) increased from 10 to 180 s after parturition.

Many species exhibit ontogenetic changes in behavior (Nagayama et al. 1986; Hopkins et al. 2011). We documented ontogenetic shifts toward longer durations of immobile defensive behavior in both male and female *H. nasicus*. Why did juvenile *H. nasicus* only death-feign for a short time? Gregory (2008) found that young Grass Snakes (*Natrix natrix*) were more likely to flee than adults and suggested that immobility is a riskier antipredator defense strategy for small snakes. The elements of death-feigning that deter would-be predators are unknown, but if these change with age, then the effectiveness of the behav-

ior might be reduced at small sizes. Ontogenetic changes in predation pressure might also be responsible. Although no sexual differences in juvenile behavior were observed, interspecific variation in sexual differences has been documented in captive neonate snakes of the genera *Nerodia* and *Thamnophis* (Scudder & Burghardt 1983; Herzog et al. 1989).We suggest that sexual differences might also be present in juvenile *H. nasicus* and other *Heterodon*, particularly because of innate sexual dimorphism in adrenal gland size (Smith & White 1955; Mohammadi et al. 2013), but these effects will require further study to elucidate.

Ontogenetic shifts in foraging behavior are often observed in snakes (Lind & Welsh 1994; Shine et al. 2001). Corresponding ontogenetic shifts in diet are common in snakes (Shine & Wall 2007), and *H. nasicus* is no exception (A. M. Durso & S. J. Mullin, own data). Non-foraging behavior and diet have been shown to covary in a variety of organisms (Bryant & Atema 1987; Brashares et al. 2000; Liang et al. 2008), but rarely in snakes (Mori & Burghardt 2000). Differences in prey toxicity might influence antipredator behavior via sequestration (Savitzky et al. 2012) or other physiological phenomena (Mohammadi et al. 2013). *Heterodon* are known to prey on several species of toxic amphibians, although there is scant evidence that *H. nasicus* at our site incorporate these species into their diet (A. M. Durso & S. J. Mullin, own data). A different relationship between defensive behavior and size might be expected at a site where snakes feed more heavily on toxic prey (Mori & Burghardt 2000; Hutchinson et al. 2013).

Differences in microhabitat, particularly between those that afford different opportunities to seek cover or escape, are predicted to affect the behavior of occupants (Main 1987), although relatively few studies have examined variation in antipredator behavior among habitats. In contrast to findings that some prey species remain immobile for longer periods when their surroundings present few escape opportunities (Hennig et al. 1976; Ewell et al. 1981), microhabitat was not important in determining the duration of or latency to death-feigning of *H. nasicus*, when compared with sex, size, and temperature. Almost all juvenile snakes were found in open microhabitats. Differences in habitat use between juvenile and adult snakes, and the associated differences between juvenile and adult snake behavior, likely overwhelmed any measurable effects of microhabitat on snake behavior, and manipulative experiments will be required to disentangle the effects of size and microhabitat on defensive behavior of this species.

Temperature has profound impacts on behavioral performance of ectotherms (Huey 1982) and is known to affect the latency to initiation of defensive behavior in a variety of ectotherms (Brodie & Russell 1999; Gomes et al. 2002; Gerald 2008). Because this study took place in the wild, snakes were able to exercise behavioral thermoregulation and were not exposed to temperatures outside their normal thermal range. Nevertheless, our snakes exhibited greater recalcitrance to death-feign when colder, including four individuals that did not death-feign (Fig. 3), all of which were encountered at temperatures ≤20°C, which is below the activity range reported by Platt (1969). This is inconsistent with the prediction that ectotherms are expected to use passive antipredator defenses when cold because of energetic limitations. This prediction is based primarily on studies in captivity, however, where animals were exposed to temperatures above and below their normal range, inducing thermal stress. Furthermore, strong thermal dependency of performance is expected only when activity physiology and not motivation sets limits to performance (Gomes et al. 2002), which is probably not the case in wild *H. nasicus*. Because even the warmest snakes did not flee, it might be that more active defensive behaviors are not used by *H. nasicus* even when thermal limitations are not present. Captive Japanese Grass Snakes (*Rhabdophis tigrinus*) exhibited passive defensive responses more frequently at low temperatures (Mori & Burghardt 2001). Similarly, Gerald (2008) found that captive juvenile Brownsnakes (*Storeria dekayi*) were more likely to feign death and did so for longer durations at higher temperatures. Differences in predator activity might also influence the likelihood that *H. nasicus* will employ defensive behavior; some salamanders are most responsive to snake tongue-flicks under thermal conditions when snake predators are most likely to be encountered (Brodie et al. 1991).

Less costly stationary defensive behaviors, such as releasing musk or feces, are probably more important at temperatures suboptimal even for death-feigning. However, we found no relationship between temperature and defecation in our snakes. Burghardt (1991) reported that defecation was more common among captive juvenile *H. platirhinos* that did not feign death than among those that did. Our inability to detect such a pattern might have to do with the link between feeding history, which we could not quantify, and defecation.

Extrinsic factors appeared to play a greater role in regulating latency to death-feigning behavior, whereas a combination of intrinsic and extrinsic factors affected the behavior's duration. Investigating the effects of multiple intrinsic and extrinsic factors simultaneously is necessary to draw relevant conclusions about the evolution and function of animal defensive behaviors. Studies of animal behavior in captivity are limited in their ability to explain the influence of a natural environment on behavioral ecology. Our goal was to examine defensive behavior of *Heterodon* in the wild to understand the influence of population-level variation and relevant abiotic factors. We documented substantial variation, much of which was explained by interactions of intrinsic (sex, size) and extrinsic (temperature) factors. The relationship among these factors apparently is complex, and further investigation is needed to elucidate their roles. Although there are limitations to studies of animal behavior in the wild, we anticipate that our findings will be useful in formulating hypotheses for future studies of immobile defensive behavior in snakes. Such findings can be generalized to other taxa that exhibit stationary defensive behaviors with varying or unknown functions, including crustaceans (O'Brien & Dunlap 1975), fishes (Wells et al. 2005), amphibians (Brodie et al. 1974; Toledo et al. 2010), and even humans (Volchan et al. 2011). A better understanding of the physiology and population ecology of *Heterodon* and other snakes with convergent traits will help uncover the complex determinants of variation in immobility behavior.

Acknowledgements

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