

## Is the exploratory behavior of *Liolaemus nitidus* modulated by sex?

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**Abstract.** Chemoreception is an important sensory modality used by lizards to assess their environments and to communicate. However, despite growing information regarding chemoreception in this taxon, its modulation by sex has been little explored, except in researches directly focused on reproductive aspects. In this study, we compared the responses of females and males of the Iguanid lizard *Liolaemus nitidus* to scents from conspecifics of the same sex, themselves (own), a predator, and a control. The only stimulus that induced different responses between sexes was the scent of conspecifics; males reacted sooner than females to these scents in agreement with their lower tolerance of potential sexual competitors. The similar ecology of the sexes may explain the similarities in their responses to the other scents we tested. However, independent of the scents, we found major behavioral differences between the sexes (e.g. males always tail waved for longer), pointing intrinsic sexual variation in behaviors associated to exploration.

**Keywords.** Chemical recognition, Sexual variation, Ecology, Predation risk, Tail waving

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### INTRODUCTION

Lizards are highly dependent on the chemical modality to communicate as well as to explore and assess their environments, depending heavily for this on the vomeronasal organ (Filoramo and Schwenk, 2009; Mason and Parker, 2010). The tongue collects molecules from the environment and brings them to the vomeronasal organ, and the rate of tongue-flicking is usually used as a bioassay for chemorecognition (Mason and Parker, 2010). Using this assay it has been shown that lizards discriminate between scents of different conspecifics (Moreira et al., 2008), and between conspecifics and congeneric spe-

cies (Labra, 2011). More specifically, males can assess the competitive abilities of potential opponents (Labra, 2006), as well as the reproductive condition of females (Head et al., 2005), while females can assess the quality of males (Martín and López, 2006) and discriminate their own offspring (Main and Bull, 1996). In non-social contexts, lizards are able to detect areas scented by prey (Labra, 2007; Besson et al., 2009) or predators (Lloyd et al., 2009). Results obtained by tongue-flicks have also been confirmed or reinforced by including other behavioral traits, such as headbobs (Labra, 2006), tail displays (Alonso et al., 2010), bites (Khannoon et al., 2010), slow motion (Labra and Niemeyer, 2004) and time in motion (Labra, 2007).

Despite the increasing volume of information on lizard chemoreception (Mason and Parker, 2010), almost no effort has been put into exploring the role of sex in this reception (see Sampedro et al., 2008), except in studies directly focused on reproductive behavior: sexual selection (Martín and López, 2008) and species recognition (Barbosa et al., 2006; Gabirot et al., 2010). These, as well as studies in taxa such as mammals (Dorries et al., 1995; Baum and Keverne, 2002), have showed that sexual variation in response to scents is related to reproduction, which has been correlated with sexual dimorphism in brain areas and neural circuits involved in chemoreception (lizards: Sampedro et al., 2008; mammals: Suárez and Mpodozis, 2009; Stowers and Logan, 2010). However, this sexual dimorphism does not necessarily imply sexual variation in the chemorecognition of non-reproductive scents. Food, for example, might trigger the same behavior in both sexes (Stowers and Logan, 2010).

To shed some light on whether sex modulates lizards' chemorecognition, we compared the responses of males and females of the Iguanid lizard *Liolaemus nitidus* to non-reproductive scents normally found in the environment: from themselves, a snake predator, and a control (free of scents from *L. nitidus* or other species). We also compared the sexes' response to conspecific of the same sex, which can be important in intersexual competition.

## MATERIALS AND METHODS

### *Animals and their maintenance*

*Liolaemus nitidus* is a common and widespread species from central Chile (Mella, 2005). During the austral spring of 2009 (November - December) we collected lizards (10 males and 10 females) by noose in "El Tabo" (33° 29'S- 77° 38'W), central Chile. The mean snout-vent length of males and females were  $82.71 \pm 3.67$  (SE) and  $74.24 \pm 2.5$  mm, respectively. Four individuals (1 male and 3 females; snout-vent length:  $60.9 \pm 3.17$  cm) of the snake *Philodryas chamissonis* were collected from different localities in central Chile, far away (~ 120 - 150 km) from "El Tabo". This snake species is one of two species that inhabit central Chile, with the most saurophagus habits of these species (Jaksic et al., 1982), and it preys on *L. nitidus* (Lobos et al., 2009). In the laboratory, individuals of both species were sexed, weighed, and their snout-vent lengths were measured. Lizards were placed in an indoor vivarium equipped with halogen lamps that kept the room with conditions similar to a typical local summer day: temperature between 12 and 32°C and a photoperiod of 13L:11D. Animals were housed individually in plastic enclosures (42 x 29 x 24 cm) with a frontal window (10 x 14 cm) covered with plastic mesh. The lids of the enclosures were partially replaced by a plastic mesh (16 x 29 cm), which allowed more light and ventilation, and added extra surface to climb. Enclosures had a substrate of sand (3 cm), a wooden stick used by lizards to climb and

bask, and two bowls, one for water and the other, inverted, to provide a shelter and a basking place. Water was supplied *ad libitum* and food (mealworms) was supplied every other day (always dusted with vitamins). Snakes were maintained in a separate room in identical conditions to those used for lizards (i.e. terraria, photoperiod and temperature). They were fed once per week with a mouse of approximately 21% of snake weight (similar to the weight of an adult *L. nitidus*), as was approved by the bioethical committee.

### *Experiment design*

Animals remained in their enclosures for one week without disturbance to allow them to acclimate to the experimental conditions and to release scents, since enclosures were used for substrate-borne scents. For the experiments, the focal individual was removed from its enclosure and held in a cloth bag for 10 min to reduce handling-associated stress (Labra, 2011). Thereafter, the bag was carefully opened allowing the animal to move freely into the experimental enclosure. Lizards were tested individually and randomly in enclosures used by: (1) a conspecific of similar size and same sex as the tested lizard, (2) the tested lizard (own), (3) an individual of *P. chamissonis* (snake) and (4) an unused enclosure (control) without scents from a heterospecific or conspecific, which contained new sand of the same type as the maintenance enclosures. For the experiments, the inhabitant of the experimental enclosure was removed just before the trial, together with the bowls and the stick. Between trials, control enclosures were rinsed with abundant water containing a bit of detergent to eliminate residual chemical traces from the tested lizard; the sand was replaced. Potential biases in behavior due to variations in body temperature were avoided by recording the cloacal temperature of the tested lizard at the end of the trial. If values were not close ( $\pm 3^\circ\text{C}$ ) to the mean selected body temperature of the species ( $35^\circ\text{C}$ ; Labra, 1998), the trial was disregarded and repeated later. Lizards were subjected to one trial per day, and at the end of the experiments, they were returned to their own enclosures in which they were kept undisturbed for at least three days.

After the focal lizard was placed in the experimental enclosure, we recorded the latency to the first tongue-flick, i.e. time elapsed between the introduction of the lizard into the enclosure and the initiation of the first tongue-flick (see below). Once the lizard licked, we filmed its behavior for 10 min with an 8-mm digital video camera placed 50 cm above the terrarium. From the videos, and based on previous studies (e.g., Labra and Niemeyer, 2004; Labra, 2006, 2007), we recorded the following variables: (1) motion time: the total time that lizards made adjustments of the body posture, displacements, or head movements (scanning), excluding any motion arising from the behaviors listed below. (2) Latency to the first movement of the tail: time elapsed between the first tongue-flick and the first tail movement, and (3) tail waving: the total time that the entire tail, or its posterior portion, was moved rapidly from side to side. These three variables were recorded directly with a stopwatch. (4) Tongue-flicks: the number of protrusions and rapid retractions of the tongue, regardless of whether it touched the substrate or was waved in the air. Other behaviors (gaping, digging, slow motion, headbobs, marking behaviors, and self-licking) were observed, but their low frequency precluded any further test, although one of this is discussed later.

Animals were maintained in good condition during the entire period of experimentation and were returned to their capture sites at the end of the study.

### *Statistical analysis*

To achieve normality of residuals, latency to the first tongue-flick and number of tongue-flicks were  $\text{Log}_{10}$  and square-root transformed, respectively. For these two variables, as well as for motion time, the effects of sex, treatment, and their interaction were determined by two-way

ANOVAs with repeated measurements for treatments. Thereafter, LSD post-hoc tests were applied. Because the residuals of the two variables related to the tail did not achieve normality even after transformations, they were analyzed using the non-parametric Friedman's ANOVAs followed by Conover post-hoc tests. Sexual differences in these two variables were investigated using a Mann-Whitney test. Data are shown as untransformed mean  $\pm$  SE. Statistical significance was set at  $P < 0.05$  and all tests were two-tailed. Analyses were made with BrightStat (Stricker, 2008).

## RESULTS

Latency to the first tongue-flick was affected by sex and by its interaction with the treatment (Table 1); males had shorter latency than females (LSD test:  $P = 0.0389$ ). The interaction revealed that in conspecific enclosures, males tongue-flicked earlier than females (Fig. 1;  $P = 0.0267$ ). Motion time was only affected by the treatment (Table 1); lizards were more active in the enclosure of conspecifics than in their own or snake enclosures (Fig. 2;  $P = 0.0012$  and  $P = 0.0102$ , respectively), as well as in the control enclosure, although this was not statistically significant ( $P = 0.062$ ). The treatment also affected the number of tongue-flicks (Table 1); lizards did it less in their own enclosures than in those of conspecifics or snakes (Fig. 3A;  $P = 0.0024$  and  $P = 0.0275$ , respectively), and also less than in the control enclosure, although this was not statistically significant ( $P = 0.061$ ). The interaction between sex and treatment was also significant (Fig. 3B; Table 1); females tongue-flicked less in their own enclosures than in the enclosures of conspecifics or controls ( $P = 0.0002$  and  $P = 0.0279$ , respectively), and made fewer tongue-flicks in the snake enclosure than in conspecific enclosures ( $P = 0.0143$ ).

The latency to the first tail wave differed marginally among treatments (Friedman ANOVA  $X^2 = 7.78$ ,  $P = 0.0507$ ); lizards waved the tail sooner in the snake and control enclosures than in their own enclosures (Conover test:  $P < 0.05$ , in both cases). However, there was a clear sexual difference in this latency; males waved the tail before females (Fig. 4A). The total time that lizards waved their tails differed among treatments ( $X^2 = 10.9$ ,  $P = 0.0120$ ); this was shorter in their own than in the snake and control enclosures (Conover test:  $P < 0.01$ ). Finally, males waved the tail for longer than females (Fig. 4B).

**Table 1.** Repeated measures analysis of variance, testing for the effects of sex, treatment (conspecific of the same sex, own, snake, and control enclosure), and their interaction on three response variables, recorded in *Liolaemus nitidus* with statistically significant values in bold.

	df	Latency to the first tongue-flick		Motion time		Number of tongue-flicks	
		F	P	F	P	F	P
Sex	1,54	4.962	<b>0.0389</b>	1.620	0.2193	0.727	0.4050
Treatment	3,54	0.236	0.8709	4.305	<b>0.0086</b>	3.600	<b>0.0191</b>
Sex x Treatment	3,54	2.981	<b>0.0393</b>	1.846	0.1498	3.012	<b>0.0379</b>

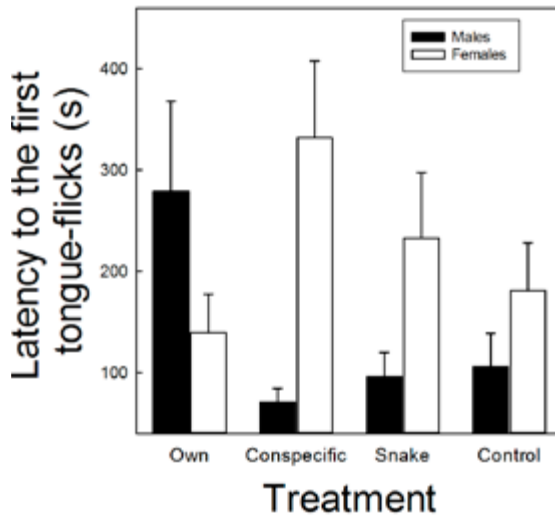


Fig. 1. Mean latency to the first tongue-flick (+SE; seconds) exhibited by males and females in four experimental conditions.

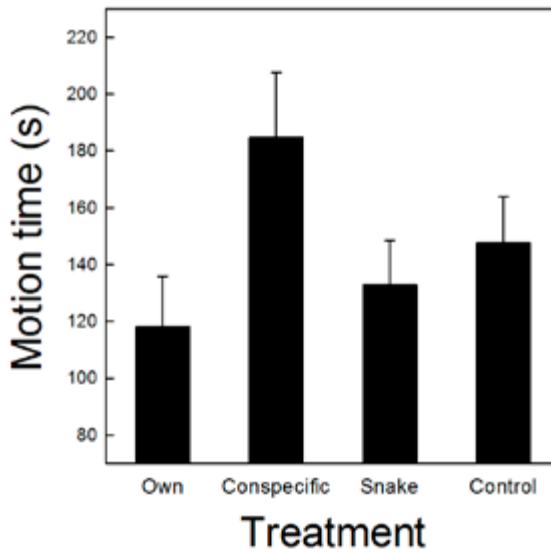
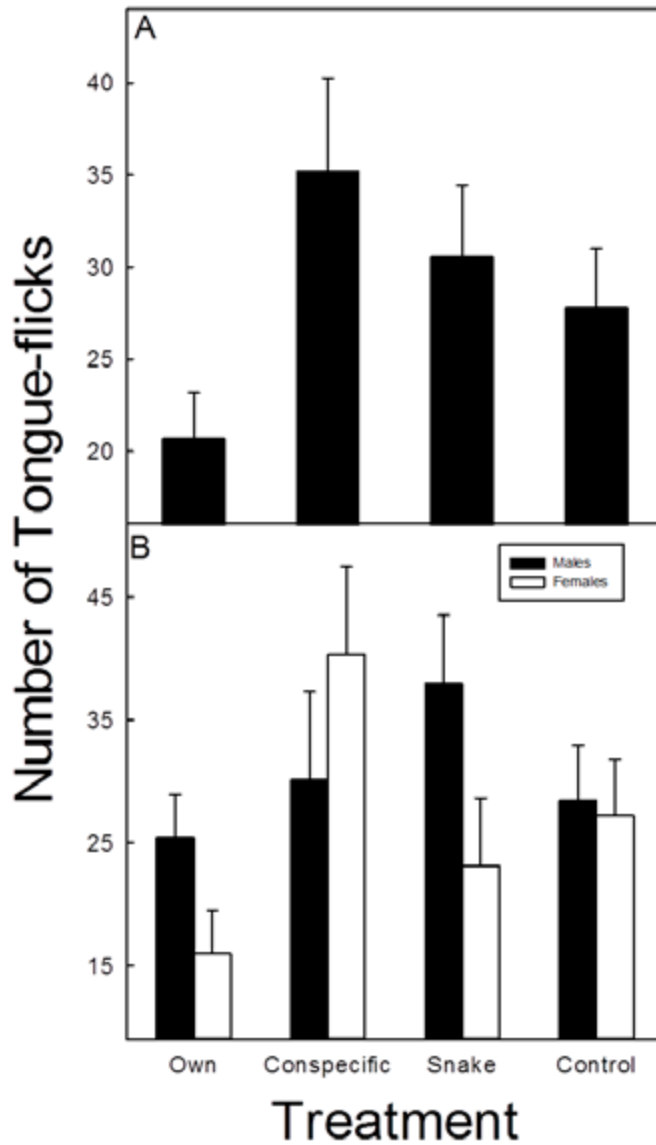


Fig. 2. Mean total motion time (+ SE; seconds) exhibited by *L. nitidus* in four experimental conditions.

## DISCUSSION

Females and males of *L. nitidus* shared many similarities in their behavioral responses to the different chemical environments, which could be a consequence of their similar ecologies (see below). Interestingly, however, independent of the actual scents they



**Fig. 3.** Mean total number of tongue-flicks (+ SE) displayed by *L. nitidus* in four experimental conditions. A. Total average. B. Data separated by sex.

encounter, the sexes showed major differences in the way they behave in the different environments. Below, we discuss the responses related and unrelated to the encountered chemical stimuli separately.

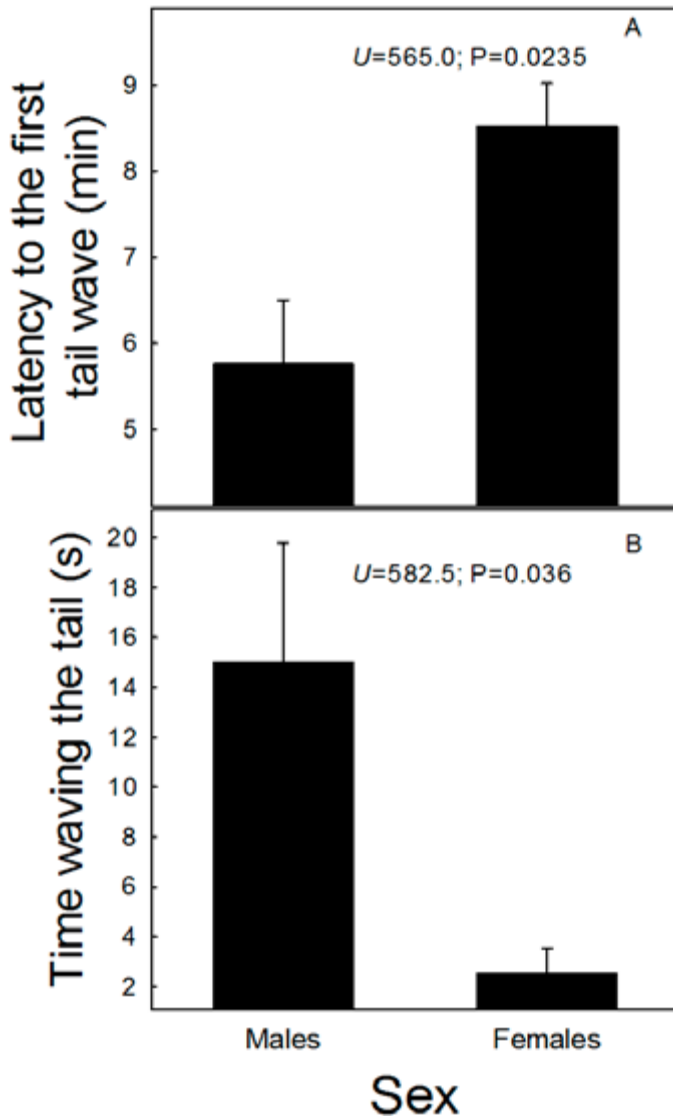


Fig. 4. Mean A. Latency to the first tail wave (+SE; minutes) and B. Total time waving the tail (+ SE; seconds) exhibited by males and females of *L. nitidus*. The results of the Mann-Whitney tests are shown.

I- Chemorecognition of different scents

*Conspecific.* The only stimulus that caused different responses between sexes was the scent of conspecifics, which triggered faster chemical exploration in males (i.e. shorter latency to the first tongue-flick). This sexual difference can be consequence of males experiencing a higher selective pressure to recognize and react against conspecifics of the same

sex, considering that male home ranges do not overlap, while those of females overlap by approximately 12% (Fox and Shipman, 2003). In this regard, a faster reaction of an invader male (the tested lizard) to scents found in the “territory” of another male speeds up the collection of information, which may allow the invader to assess the fighting abilities of the territory owner and react accordingly (Labra, 2006). Interestingly, Cooper et al. (1996) found that both sexes of *Cordylus cordylus* tongue-flicked more to conspecifics of the same sex, which was attributed to the high territoriality of both sexes in this species. Thus, we can hypothesize that territoriality may be a modulator of response to scents of conspecific of the same sex, i.e. higher territoriality, stronger response to these scents.

What explains the different reactions of the sexes of *L. nitidus* to conspecific scents before the first investigation with the tongue? Scents are a blend of compounds with different degrees of volatility (Weldon et al., 2008), and it has been proposed that the latency to the first tongue-flick can be modulated by olfaction through the nose of the volatile fraction of the blend (Cowles and Phelan, 1958). On this background, our hypothesis is that sexes may differ in the production of volatile compounds that activate olfaction, with males producing a different or more concentrated blend of certain volatile compounds, which then prompts a faster recognition, and initiation of the exploration. For example, in *Acanthodactylus boskianus* males and females differ in the chemical composition of the femoral glands, which have pheromonal activity (Khannoon et al., 2011). We know that there are interspecific and intraspecific differences in the chemical composition of the scents from preloacal secretions in several species of *Liolaemus*, and these secretions are only present in males of the analyzed species (Escobar et al., 2001). But we do not know about sexual differences in other sources of scents (Labra et al., 2002). Another non-exclusive hypothesis for this difference in latency to the first tongue-flick is that sexes differ in their sensibility to the volatile compounds produced by conspecifics of the same sex, with males being more sensitive than females to compounds coming from individuals of the same sex. Results from *Iberolacerta cyreni* partially support this hypothesis; sexes differ in their responses to different chemical compounds present in males’ femoral glands (Martín and López, 2008). Which of these hypotheses are correct will need further investigations based on chemical isolation and behavioral testing of pheromonal compounds from males and females.

Finally, the observation that both sexes moved more in enclosures of conspecifics may be interpreted as attempting to escape of the “territory” of an unfamiliar individual.

*Self-recognition.* A lower number of tongue-flicks toward the own vs. other scents is clear evidence of self-recognition (Labra, 2008). The absence of a sex effect in self-recognition suggests that sexes may have the same capability to recognize familiar (own) scents. However, some caution is required in interpreting this result, considering that we found an interaction between sex and treatment, indicating that self-recognition based on tongue-flicks was strongly dependent on female behavior, opening up the possibility that sexes may differ in how they process their own scents. This requires further investigation with larger sample sizes.

*Predator.* Males and females behaved similarly when confronted with snake scents, possibly a consequence of similar predation risk (Jaksic and Fuentes, 1980). Two sets of



evidence showed that lizards recognized the snake scent. First, lizards waved their tails sooner and for longer in the snake and control enclosures, as compared to their own enclosures. These two conditions, snake and control, would be the most threatening, because lizards may face known (snake) or unknown (control condition) risk, and tail waving can help to deflect attacks toward the tail instead of toward the body (Telemeco et al., 2011), enabling lizards to escape by autotomizing the tail (Bateman and Fleming, 2009). Secondly, the snake scent was the only stimulus that triggered slow motion (in three individuals), which may help to reduce detectability to a predator (Labra and Niemeyer, 2004).

*Control condition.* Sexes behaved similarly in the control condition, probably a consequence of resemblance in their general exploratory behavior. It is known that explorations of environments made by lizards (i.e. total time that animals move) is positively correlated with the size of their home ranges (Verwajen and Van Damme, 2008), and both sexes of *L. nitidus* have similar home range size (Fox and Shipman, 2003). Based on this, we expected that both sexes of *L. nitidus* behave and explore similarly in novel environment. Interestingly, Cooper et al. (2001) found no sexual differences in total movement in the field in five lizard species, although they gave no comments on their territorial behavior.

## II- Exploratory behavior of the environment: sexual variation

Independent of the chemical scents found in the environment, females and males of *L. nitidus* showed three behavioral differences: latency to the first tongue-flick, latency to first tail wave, and total time waving the tail. Males started chemical exploration (tongue-flicks) sooner than females, which may suggest that they are more “eager” to explore any environment, but potentially increase their risk of being detected and attacked sooner by predators or conspecifics. Increased tail waving may then help to deflect potential attacks to the tail, allowing the individual to escape, as we discussed earlier (Bateman and Fleming, 2009; Telemeco et al., 2011). Alonso et al. (2010) found that males of the gecko *Gonatotodes albogularis* tail waved more than females, and ascribed this to sexual variation in predation rate. This explanation does not make sense for of *L. nitidus*, as both sexes experience similar predation rates (Jaksic and Fuentes, 1980), but reinforces the relevance of the ecology of the group to understand their behavior.

The fact that sexual differences were consistent across the treatments may be an indication of sexual variation in behavioral syndrome (sensu Sih et al., 2004) of *L. nitidus* (Schuett et al., 2010), as in other species. In the pygmy bluetongue lizard, *Tiliqua adelaidensis*, males directed more tongue-flicks than females to a novel burrow, but there were no difference in the time that they inspected or remain in the burrow (Fenner and Bull, 2011).

We summarize our results in *L. nitidus* by concluding that the ecology of sexes seems to be a modulator of their responses to different scents; sexes behave similarly towards scents with similar ecological meaning (non-reproductive: predator, own, and control) and differ when confronted to scents that represent something different for them (reproductive: conspecifics of the same sex). We also found behavioral differences unrelated to the perceived scents that may be evidence of different behavioral syndromes in the sexes.

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