



RESEARCH PAPER

The Attentive Spider: Search-Image Use by a Mosquito-Eating Predator

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Abstract

Evarcha culicivora, a jumping spider from East Africa, feeds indirectly on vertebrate blood by choosing blood-carrying female mosquitoes as prey. It also has an unusually complex mate-choice system. Here, we show that both sexes of *E. culicivora* can use mate-finding search images and also use prey-finding search images. In experiments, individuals were primed by seeing blood-carrying mosquitoes, primed by seeing potential mates or not primed (control: saw neither). They were then introduced into an arena where the task was to find a blood-carrying mosquito or a potential mate. In all instances, the prey or potential mates were dead individuals used as lures. The lure in the arena was either cryptic (i.e. hidden behind nylon netting and accompanied by distractors) or conspicuous (i.e. netting and distractors absent). When lures were conspicuous, the identity of the priming stimulus appeared to be irrelevant. However, when lures were cryptic, significantly more spiders found the lure that was congruent with the priming stimulus and significantly fewer spiders found the lure that was incongruent with the priming stimulus. On this basis, we conclude that the spiders were using search images for finding the lures and that search images were relevant only when the lure to be found was cryptic.

Introduction

Although human-based research has been a dominant interest in the literature on attention (e.g. Pashler 1998), biologists have also considered the role of attention in governing the behaviour of non-human animals, but by another name, 'search images'. This is a term that can be traced back to von Uexküll (1934) (see Bond 2007) but is now most often associated with the hypothesis Lukas Tinbergen used for explaining his field-based data on insectivorous birds (Tinbergen 1960). What Tinbergen envisaged was that experience with a particular prey type primes a predator to become selectively attentive to specific features of the prey (see Dawkins 1971a,b; Blough 1991; Langley 1996; Bond & Kamil 2002).

Yet much of the literature on search images (see Lawrence & Allen 1983; Guilford & Dawkins 1987) has been unclear about the distinction between selective attention and preference. 'Preference' refers to what an animal would like to eat (i.e. something that is expressed by choice behaviour), whereas 'selective attention' refers to what an animal has become cognitively prepared to detect and identify (Shettleworth 1998; Cross & Jackson 2006). When prey is conspicuous, we expect stronger expression of a predator's preferences because the cognitive demands inherent in deploying selective attention will be less severe. On the other hand, we expect selective attention to matter especially when prey is cryptic.

Jumping spiders (Salticidae) are particularly suitable subjects for research on selective-attention tasks

because their visual acuity is unrivalled by other animals in their size range (Land 1969a,b; Land & Nilsson 2002; Harland & Jackson 2004). Moreover, they have often been used in research on vision-based prey and mate identification (Jackson & Pollard 1996, 1997). For example, salticids can be tested with immobile lures instead of living prey (Jackson & Tarsitano 1993), which means we can ascertain whether they have found potential prey in the absence of movement cues and without the actions of the prey individual confounding interpretation of experimental outcome.

Here, we consider the role of selective attention in the biology of *Evarcha culicivora*, a salticid from the Lake Victoria region of East Africa. This species is unusual because it specializes in feeding on vertebrate blood, gaining access to blood indirectly by choosing blood-carrying mosquitoes as preferred prey (Jackson et al. 2005). However, satisfying this predatory preference may be especially challenging for *E. culicivora* because, although mosquitoes are plentiful in this habitat, they are vastly outnumbered (Okedi 1992) by mosquito-size non-biting midges (Chaoboridae and Chironomidae), known locally as 'lake flies'. Although *E. culicivora* eats lake flies as well as mosquitoes, the majority of its prey in nature is blood-carrying mosquitoes (Wesolowska & Jackson 2003).

However, for *E. culicivora*, predation is not the only context in which search images may be relevant. *Evarcha culicivora*'s courtship is exceptionally complex, with each sex actively courting the other (Cross et al. 2008) and with both sexes being capable of identifying and choosing mates on the basis of visual cues alone (Cross et al. 2007). Here, we consider for both sexes whether search images are used not only in the context of finding prey but also in the context of finding potential mates.

Methods

General

Our field site and laboratory were in western Kenya (Mbita Point, 0°25'S–0°30'S by 34°10'E–35°15'E, 1200 m above sea level, mean annual temperature 27°C) at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology. All spiders were from laboratory culture (F2 generation). Standard spider-laboratory procedures were adopted (see Cross et al. 2008) and all testing was carried out between 08.00 and 13.00 hours (laboratory photoperiod 12L:12D, lights on at 07.00 hours).

We ensured that the spiders had no prior exposure to mosquitoes or to conspecific individuals before use in experiments. This was achieved by rearing them on a diet of 'lake flies' collected as needed from the field (fed to satiation 3 times a week) and by keeping individuals in separate cages from which no other spiders and no mosquitoes were visible. As in earlier studies (Li & Jackson 1996; Jackson et al. 2005), a 7-d pre-trial fast was adopted for standardizing the hunger level of test spiders.

All spiders used in experiments were virgin adults (both sexes) that had matured 2–3 weeks before used in trials. For lures, blood-carrying *Anopheles gambiae* ss (Culicidae) females (hereafter referred to simply as 'mosquitoes') and virgin *E. culicivora* males and females (hereafter referred to simply as 'mates') were used. No individual of *E. culicivora* and no individual mosquito was used more than once as a test spider or as a lure. All individuals used as test spiders and all of the mosquitoes and spiders used as lures were 4.5 mm in body length (measured to nearest 0.5 mm). Mosquitoes were fed on human blood 4–5 h before being used as lures (for details, see Jackson et al. 2005).

To make lures, mosquitoes and spiders were first immobilized with CO₂ and then placed in 80% ethanol. The next day, each mosquito or spider was mounted in a life-like posture on the centre of a disc-shaped piece of cork (diameter 10 mm; thickness 2 mm). For preservation, the lure and the cork were then sprayed with a transparent plastic adhesive (Crystal Clear Lacquer; Atsco Australia Pty, Cheltenham, Victoria, Australia).

Experimental Apparatus

For distinguishing between the effects of selective attention and the effects of preference, there were two trial types, 'cryptic' and 'conspicuous' (Fig. 1a). In cryptic trials, *E. culicivora* was presented with the task of finding a mosquito lure or mate lure that was behind nylon netting and accompanied by cork discs on which no lure was mounted ('distractors'). Conspicuous trials were like cryptic trials except for the absence of the features (netting and distractors) that were used in cryptic trials to make the lure difficult to find.

We used a square arena (100 mm × 100 mm, walls 35 mm high) made of glass (Fig. 1a) and with a removable glass lid (100 mm × 100 mm). The arena was surrounded by four wooden walls (each side 140 mm long, 50 mm high, 10 mm thick). Each wall had two indentations (diameter 36 mm, depth 5 mm) and each indentation held a small Petri dish

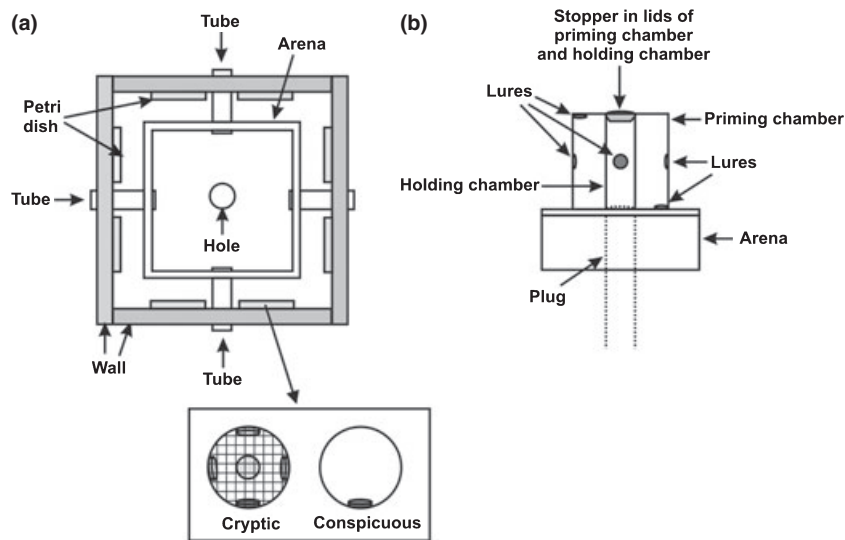


Fig. 1: Arena (not drawn to scale) made of glass. Stand (not shown) holds arena. (a) Arena viewed from above. Inset: view of cork discs from perspective of spider inside box and facing Petri dish. Cork disc on which lure is placed: shaded in drawing. Hole (diameter 25 mm): one positioned in lid (shown in drawing); other in floor of arena (not shown) directly below hole in lid. Cryptic trials: nylon netting covers dish; besides disc with lure, another four cork discs present (not shaded in drawing). Conspicuous trials: only one disc (with lure); other four cork discs absent; nylon netting absent. (b) Arrangement of holding chamber, priming chamber and plug before introducing spider into arena. Six lures (absent in control tests) inside priming chamber. Clamp holding plug not shown. Tubes attached to arena not shown.

(diameter 35 mm, height 10 mm) (i.e. there was a total of eight Petri dishes spaced around the arena). Glass tubes (length 50 mm, diameter 12 mm) fitted in holes (diameter 12 mm) on each of the four sides of the arena and protruded through holes (diameter 12 mm) in the centre of each wall. The end of each tube that faced into the arena was open. The other end was closed with a stopper. The arena and walls sat on a wooden stand (300 mm × 300 mm; wood thickness 20 mm; legs of stand 270 mm long).

In cryptic trials, each Petri dish covered five cork discs (double-sided adhesive tape used to affix each disc). One of the five discs was attached to each wall (facing the centre of the dish). The other four discs were spaced evenly around the dish rim, with one of these discs being positioned where the rim was closest to the floor of the arena ('lower rim position'). Each Petri dish was covered with nylon netting (mesh size, 1.5 mm × 1.5 mm).

In conspicuous trials, only one cork disc was attached to each Petri dish (always in the lower rim position) and the netting was absent. For the cryptic and for the conspicuous treatment, there was a lure in only one of the eight Petri dishes. Which particular dish contained the lure was decided at random. The disc on which the lure was mounted was always in the lower rim position and the lure always faced towards the arena.

Priming Apparatus

A cubical priming chamber (made of 5-mm thick glass, inner dimensions 70 × 70 × 70 mm; 25-mm hole in lid and floor) and a cylindrical holding chamber (made of 1-mm thick glass; length 70 mm, inner diameter 25 mm) were used before each test (Fig. 1b). The holding chamber (with the test spider inside) was kept within the priming chamber and both chambers sat on the arena lid. The lower end of the holding chamber was positioned in a hole in the arena lid, while the upper end was blocked by a stopper that also closed a hole in the lid of the priming chamber. The spider could not enter the arena because an upside down test tube ('plug') (diameter 25 mm) extended through a hole in the floor of the arena and pressed against the lower end of the holding chamber. The plug was held in place by a clamp under the arena and stand.

In some tests, there were no lures in the priming chamber ('control'), while in other tests ('experimental') there were six lures, one centred on each of the four walls (facing down), as well as one on the floor and one on the ceiling. The lure on the floor and the lure on the ceiling were positioned so that they faced the centre of the floor and ceiling, respectively, and each was positioned so that it was against one of the four walls (which wall decided at

random) and midway between two neighbouring walls. All six lures were made from either mosquitoes or mates.

The test spider was kept in the holding chamber for 10 min with lures in view. The plug was subsequently removed and then, immediately afterwards, a rubber stopper was inserted in the hole in the arena floor and the priming chamber was lifted away. A soft brush, pushed through the top end of the holding chamber, was used for gently nudging the test spider so that it walked quietly into the arena. Once the test spider was inside the arena, the holding chamber was removed and the hole in the arena lid was plugged with a rubber stopper (i.e. testing began).

Experimental Methods

There were two alternative criteria for recording that the test spider had 'found' the lure in the arena. One of these criteria was seeing it enter the tube closest to the location of the lure and stay inside for at least 30 s. The rationale for the 30-s proviso was that sometimes, in preliminary trials, *E. culicivora* entered a tube for a few seconds and then left. However, when any individual stayed in a tube for 30 s, it remained in this tube for at least 5 min. Moreover, any individual that subsequently left this tube never entered and remained in another tube for as long as 30 s. The other criterion was seeing *E. culicivora* press its face against a side of the arena while oriented directly towards a lure, regardless of whether it subsequently entered the tube. This second criterion was never applicable in more than 10% of the recorded instances of finding a lure for any treatment. Trials ended when *E. culicivora* found the lure or, if *E. culicivora* did not find a lure, when 60 min elapsed.

The entire apparatus was lit with a 200-W incandescent lamp positioned 400 mm overhead and there was additional ambient lighting from overhead fluorescent lamps. Between trials, the apparatus was dismantled and cleaned with 80% ethanol, followed by distilled water and then dried.

Data Analysis

Data were analysed using chi-squared tests of independence. Although Bonferroni adjustments were applied whenever there was repeated testing of the same data sets (adjusted alpha = 0.017; see Howell 2002), the outcome of applying these adjustments never altered conclusions about statistical signifi-

cance. For our experiment, the relevant data were the number of spiders that found the lure. Although data on latency are often considered for experiments on selective attention, they were not especially informative for the particular experimental design we used. In all conditions for cryptic and for conspicuous trials, the sample size for males was 200 (i.e. 2400 individual males were tested) and the sample size for females was 160 (i.e. 1920 individual females were tested).

Results

Does the Cryptic-Conspicuous Distinction Matter?

Regardless of whether they were primed with congruent lures, primed with incongruent lures or not primed, the number of spiders that found conspicuous mosquitoes or mates was significantly larger than the number that found cryptic mosquitoes or mates (Table 1; Figs 2 and 3). These findings confirm that our methods were effective at making lures difficult to find in cryptic trials and easier to find in conspicuous trials.

Does the Priming Stimulus Matter When the Lure is Conspicuous?

Regardless of whether the task was to find a conspicuous mosquito or to find a conspicuous mate, the number of spiders that found the lure after congruent priming (i.e. finding a mosquito after primed by seeing mosquitoes and finding a mate after primed

Table 1: Spiders (*Evarcha culicivora*) that found lure after being primed by a particular stimulus. Comparison of spiders that found a cryptic lure rather than a conspicuous lure

Test spider	Lure to find	n	Priming stimulus	Test of independence χ^2
Male	Cryptic vs. conspicuous mosquito	200	Mosquitoes	43.25**
		200	Mates	115.56**
		200	None	104.45**
Female	Cryptic vs. conspicuous mosquito	160	Mosquitoes	48.81**
		160	Mates	135.55**
		160	None	87.56**
Male	Cryptic vs. conspicuous mate	200	Mosquitoes	168.05**
		200	Mates	79.45**
		200	None	107.52**
Female	Cryptic vs. conspicuous mate	160	Mosquitoes	116.65**
		160	Mates	58.91**
		160	None	104.61**

**p < 0.001.

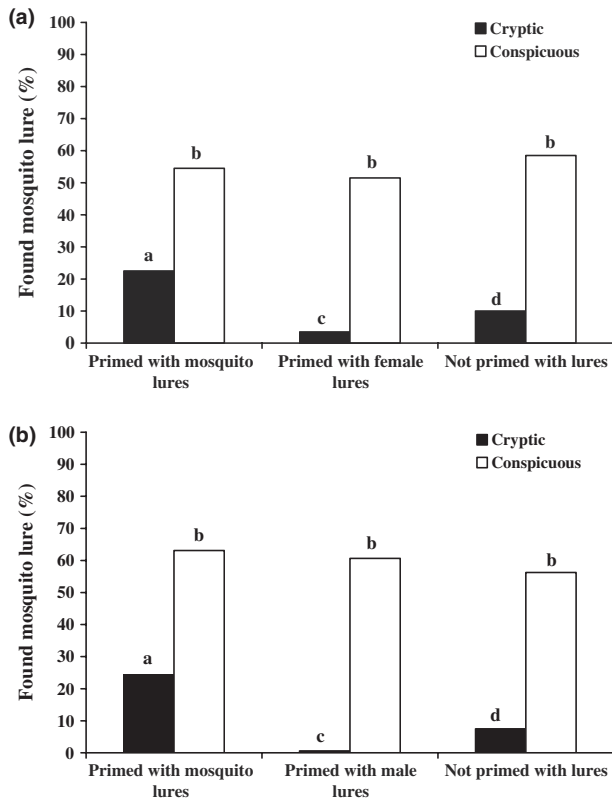


Fig. 2: *Evarcha culicivora* males (a) and females (b) that found mosquitoes. Mosquitoes were cryptic or conspicuous. Before entering arena, spiders were primed by seeing mosquitoes, primed by seeing mates or not primed. Different letters above bars denote statistical significance; same letters denote non-significance. Statistical significance was not affected by Bonferroni adjustments.

by seeing mates) was not significantly different from the number that found the lure after incongruent priming or after no priming (Table 2; Figs 2 and 3).

Does the Priming Stimulus Matter When the Lure is Cryptic?

Regardless of whether the task was to find a cryptic mosquito or to find a cryptic mate, significantly more spiders found the lure after congruent priming than after incongruent priming or after no priming (Table 2; Figs 2 and 3).

Discussion

The appearance of blood-carrying mosquitoes and the appearance of potential mates are both particularly salient to *E. culicivora* (Jackson et al. 2005; Cross et al. 2007). In this study, we were interested in whether *E. culicivora* adopts prey-specific and

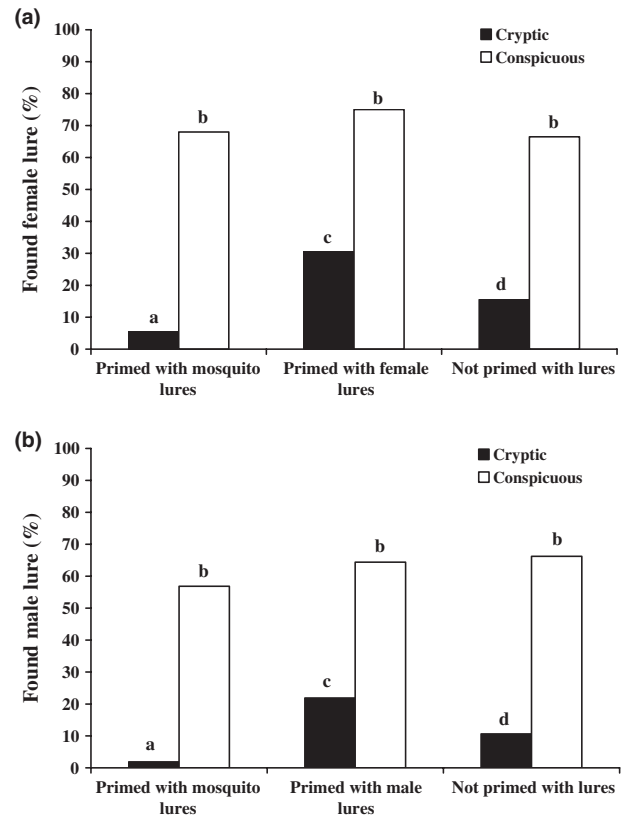


Fig. 3: *Evarcha culicivora* males (a) and females (b) that found mates. Mates were cryptic or conspicuous. Before entering arena, spiders were primed by seeing mosquitoes, primed by seeing mates or not primed. Different letters above bars denote statistical significance; same letters denote non-significance. Statistical significance was not affected by Bonferroni adjustments.

mate-specific search images. Search-image use is defined by selective attention, not preference (Shettleworth 1998; Bond & Kamil 2002; Cross & Jackson 2006). This means that, for demonstrating selective attention, experimental methods need to probe an animal's ability to identify objects when detection is difficult. We achieved this in our study by first showing that *E. culicivora* has less difficulty finding lures that are conspicuous and more difficulty finding lures that are cryptic. We also showed that it was only in the cryptic trials where significantly more spiders found a lure after congruent priming than after incongruent priming. When lures were conspicuous, no effect of priming was evident. On this basis, we conclude that *E. culicivora* makes use of prey-finding and mate-finding search images.

Besides having become more effective at finding a congruent stimulus after priming, *E. culicivora* also became less effective at finding an incongruent stimulus after priming. For example, when the task

Table 2: Spiders (*Evarcha culicivora*) that found lure after being primed by a particular stimulus. Comparison of spiders that found lure when priming stimulus varied

Test spider	Lure to find	n	Priming stimulus	Test of independence	
				χ^2	p
Male	Conspicuous mosquito	200	Mosquitoes vs. mates	0.36	0.548
		200	Mosquitoes vs. no priming	0.65	0.420
		200	Mates vs. no priming	1.98	0.159
Female	Conspicuous mosquito	160	Mosquitoes vs. mates	0.21	0.645
		160	Mosquitoes vs. no priming	1.57	0.210
		160	Mates vs. no priming	0.63	0.427
Male	Conspicuous mate	200	Mates vs. mosquitoes	2.40	0.121
		200	Mates vs. no priming	0.10	0.749
		200	Mosquitoes vs. no priming	3.49	0.062
Female	Conspicuous mate	160	Mates vs. mosquitoes	1.89	0.170
		160	Mates vs. no priming	2.97	0.085
		160	Mosquitoes vs. no priming	0.12	0.725
Male	Cryptic mosquito	200	Mosquitoes vs. mates	31.92	<0.001
		200	Mosquitoes vs. no priming	11.48	<0.001
		200	Mates vs. no priming	6.71	0.001
Female	Cryptic mosquito	160	Mosquitoes vs. mates	41.26	<0.001
		160	Mosquitoes vs. no priming	17.00	<0.001
		160	Mates vs. no priming	9.70	0.002
Male	Cryptic mate	200	Mates vs. mosquitoes	42.34	<0.001
		200	Mates vs. no priming	12.70	<0.001
		200	Mosquitoes vs. no priming	10.64	0.001
Female	Cryptic mate	160	Mates vs. mosquitoes	30.58	<0.001
		160	Mates vs. no priming	7.44	0.007
		160	Mosquitoes vs. no priming	10.45	0.001

was to find a cryptic mate, significantly fewer spiders found it after they were primed by seeing mosquitoes rather than after no priming. This finding is interesting in the context of capacity limitations. Similar trade-offs and interference effects (Pietrewicz & Kamil 1979; Bond 1983; Dukas & Kamil 2000; Kamil & Bond 2006) are known from research on much bigger animals, such as birds and mammals, suggesting that selective attention is generally a cognitively demanding task (see Desimone 1998; Pashler 1998). We might envisage cognitive resources being tied up when an animal is selectively attentive to objects of one type, and that having fewer free cognitive resources impairs an animal's ability to detect and identify other salient objects. Yet it is currently difficult to say what these cognitive resources might actually be and exactly why attention should be especially demanding. However, our working hypothesis is that capacity limitations are especially severe for an animal with a spider-size brain (see Cross & Jackson 2006) and this, in turn, may make *E. culicivora* an especially suitable animal for future research on the mechanisms underlying selective attention.

There has been one other study (Jackson & Li 2004) showing search-image use by a salticid, this

being with *Portia labiata*, a species that prefers other spiders as prey (Li et al. 1997). Rather than *P. labiata* finding either a prey item or a potential mate, its task was instead to find one or the other of two prey-spider species (Jackson & Li 2004). However, there were basic similarities between the experimental findings from using *P. labiata* and the experimental findings from using *E. culicivora* in the present study. For example, more individuals of *P. labiata* found the prey when priming was congruent, but fewer found the prey when priming was incongruent.

Yet there were also some important differences. When *P. labiata* was primed, it was by interacting with, and by eating, living prey (Jackson & Li 2004). With this method of priming, there was no way to rule out the possibility that, for *P. labiata*, sensory modalities other than vision (e.g. olfaction) were of primary importance. However, in our experiments using *E. culicivora*, we used immobile lures that were separated by glass from each test spider and this precluded access to any sensory modality other than vision during priming. There have been other search-image studies that have precluded sensory modalities other than vision, including experiments based on using photographic slides (e.g. Pietrewicz & Kamil 1979) and, more recently, based on using

virtual prey generated by computer software (e.g., Langley 1996; Bond & Kamil 2002), but feeding was still part of the procedure.

This study is unconventional for search-image research in another way. Training is usually an integral part of the methods used in search-image studies, with the study animal envisaged as acquiring search images by perceptual learning after repeated encounters with a particular type of prey. Our experiments using *E. culicivora* were considerably different, as there was only a single experience with a priming stimulus. Moreover, the test spiders had no opportunity to mate or eat during priming, and the only possible reinforcement they could have received was from seeing the priming stimulus. Yet they became selectively attentive to the priming stimulus. This suggests that, instead of being trained to identify the visual features of prey or mates through learning, *E. culicivora* called up an innate (pre-existing) search image when primed by seeing prey or potential mates.

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