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Olfactory search-image use by a mosquito-eating predator

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By choosing blood-carrying mosquitoes as prey, *Evarcha culicivora*, an East African salticid spider, specializes at feeding indirectly on vertebrate blood. It also has an exceptionally complex mate-choice system. An earlier study revealed that search-image use assists *E. culicivora* in finding prey and mates when restricted to using vision alone. Here we show that search-image use assists *E. culicivora* in finding prey and mates when restricted to using olfaction alone. After being primed with prey odour or mate odour (control: not primed with odour), spiders were transferred to an olfactometer designed to test ability to find a prey-odour or mate-odour source that was either ‘cryptic’ (i.e. accompanied by a masking odour source, *Lantana camara*) or ‘conspicuous’ (no *L. camara* odour). When tested with conspicuous odour, the identity of the priming odour had no significant effect on how many spiders found the odour source. However, when tested with cryptic odour, significantly more spiders found the odour source when primed with congruent odour and significantly fewer spiders found the odour source when primed with incongruent odour.

Keywords: cognition; mosquitoes; olfaction; Salticidae; selective attention

1. INTRODUCTION

‘Selective attention’ has been a topic of long-standing interest in cognitive psychology (see Pashler 1998) and, although biologists usually refer to this by another name, ‘search images’ (Tinbergen 1960; Bond 2007), they have often blurred the distinction between an animal using selective attention and an animal expressing preferences. Yet, these are two different things (see Shettleworth 1998). When considering predators, for instance, ‘preference’ refers to what an animal is strongly motivated to eat and ‘selective attention’ (or ‘search images’) refers to what an animal has become especially prepared to detect and identify. This distinction has important implications for experimental design because, when prey is conspicuous, the cognitive demands inherent in deploying selective attention should be less severe. This, in turn, means we can expect stronger expression of a predator’s preferences (‘motivation’). It is when prey is cryptic that we expect selective attention to matter the most.

Consistent with the term ‘image’, it may be unsurprising that most search-image studies have considered vision-based detection and identification. The expression ‘olfactory search images’ has sometimes appeared in the literature (Nams 1991, 1997; Gazit *et al.* 2005; see also Melcer & Chiszar 1989) but not explicitly in the context of selective attention. Perhaps the cryptic–conspicuous distinction is particularly elusive when considering olfaction. Nams (1991), for example, argued that ‘cryptic’ is a concept that applies more to vision than to the other senses. Yet, the basic idea when using the term ‘cryptic’ is that something becomes hard to detect and identify, and we know that this can be achieved in experiments where olfaction is the sensory modality (Schröder & Hilker 2008; Cross & Jackson 2009*a*). Olfaction is used by many different animals in many different contexts (Wyatt 2003) and, therefore, it is important to consider whether animals use selective olfactory attention as well as selective visual attention (e.g. Chittka & Raine 2006).

Evarcha culicivora may be an especially suitable subject for experiments on search-image use. This is an unusual jumping spider (Araneae, Salticidae) from East Africa that, by preferring blood-carrying mosquitoes as prey, specializes at feeding indirectly on vertebrate blood (Jackson *et al.* 2005). It is also unusual for having exceptionally complex courtship behaviour, with each sex actively making mate-choice decisions (Cross *et al.* 2007, 2008). Salticids are known for having unique, complex eyes and for vision based on exceptional spatial acuity (Land & Nilsson 2002), but previous research has shown that *E. culicivora* can identify opposite-sex conspecifics (i.e. potential mates; Cross & Jackson 2009*b*; Cross *et al.* 2009), as well as blood-carrying mosquitoes (Jackson *et al.* 2005), not only by sight alone but also by odour alone (acoustic and seismic signals ruled out by trials using immobilized prey). Moreover, recent research (Cross & Jackson 2010) has shown that search-image use assists *E. culicivora* in finding prey and mates when restricted to using vision alone, but whether *E. culicivora* also adopts olfactory search images has not been investigated before. Our hypothesis is that *E. culicivora* uses olfactory search images for finding prey and mates.

2. MATERIAL AND METHODS

(a) *General*

Our field site and laboratory were in western Kenya (Mbita Point; ICIPE, Thomas Odhiambo Campus). Testing was

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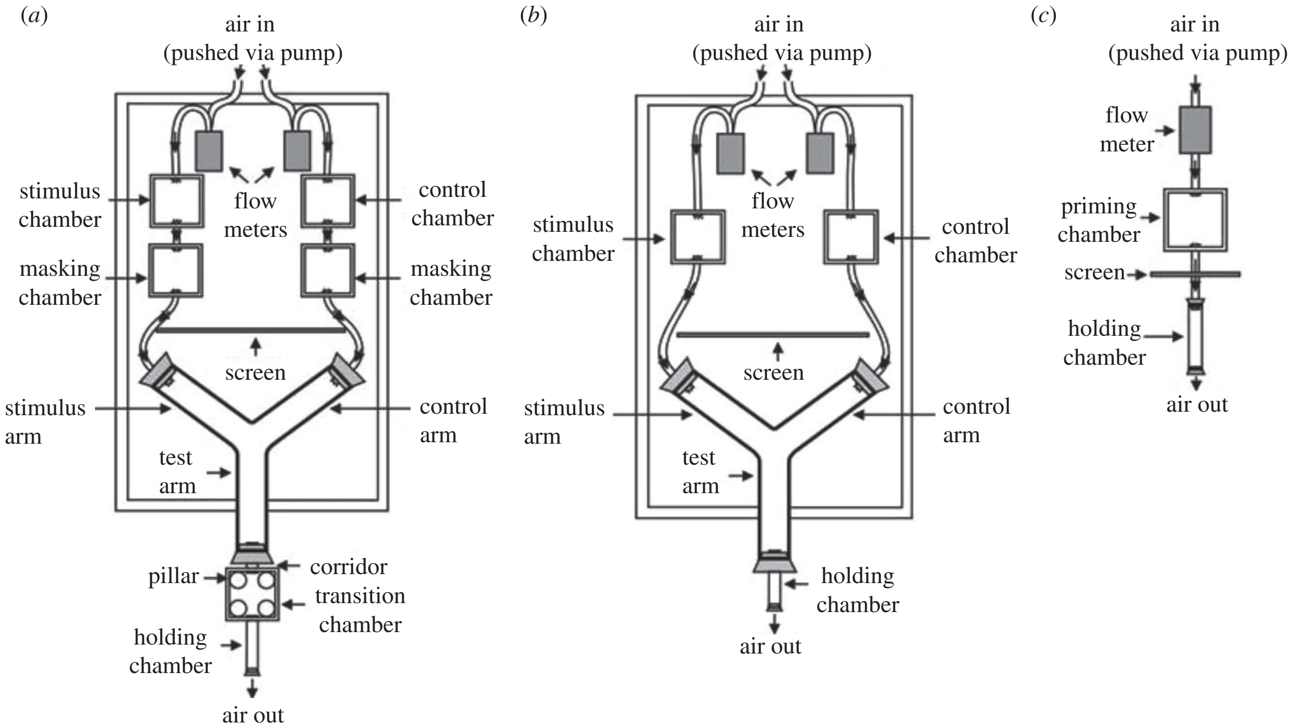

Figure 1. Apparatus (not to scale) used for investigating olfactory search images by *Evarcha culicivora*: (*a*) cryptic trials, (*b*) conspicuous trials, (*c*) how holding chamber is attached to priming chamber. Arrows: direction of airflow. (*a*) Before testing begins, test spider was placed in holding chamber (attached to transition chamber). Start of trial: test spider enters test arm by going through corridor, thereby gaining access to stimulus arm and control arm. (*b*) Start of trial: test spider in holding chamber; open end of chamber inserted in stopper, providing test spider with access to test arm.

carried out between 08.00 and 13.00 h (laboratory photoperiod 12L : 12D, lights on at 07.00 h). All spiders were from laboratory culture (F2 generation) with standard spider-laboratory procedures being adopted (see Cross *et al.* 2008).

No test or source spiders had seen, smelled or interacted with mosquitoes or with conspecific individuals before being used in experiments. Each individual was kept in a separate cage from which no other spider or mosquito was visible. Male and female spiders were housed in separate rooms. They were fed to satiation three times a week on 'lake flies' (non-biting midges: Chironomidae and Chaoboridae) that were collected as needed from the field. As in an earlier study (Jackson *et al.* 2005), hunger level was standardized by a 7-day pretrial fast for test spiders.

All mosquitoes used in experiments were *Anopheles gambiae ss* females (virgin: body length, 4.5 mm) that were fed on human blood 4–5 h before being used (for details, see Jackson *et al.* 2005). All test and source spiders were adult males and females (virgin: body length, 4.5 mm) that had matured two to three weeks beforehand. No individual of *E. culicivora* or of *A. gambiae* was used more than once as a test spider or as an odour source. For any given treatment, no more than five spiders were ever derived from the same two parent spiders.

(b) *Experimental methods*

The way the apparatus (figure 1) was set up depended on whether the odour was cryptic or conspicuous, but the basic components of the apparatus were the same for the two treatments.

There was a 'Y maze' made of glass, with the stem of the Y being the 'test arm', one of the forks of the Y being the 'control arm' and the other fork being the 'stimulus arm' (length of each arm, 90 mm; internal diameter, 20 mm). In both treatments, a 'stimulus chamber' containing 20 blood-fed mosquitoes or a 'mate' (one adult conspecific male or female) was connected to the stimulus arm. A 'control chamber' (empty) was connected to the control arm of the Y. Before entering the Y, the test spider was kept in a 'holding chamber' where it was exposed to prey or mate odour from a 'priming chamber'.

The priming chambers, when they were used for presenting mate odour, as well as all holding chambers, were cylindrical and made of 1 mm thick glass (length, 90 mm; inner diameter, 20 mm), but all other chambers were cubical and made of 5 mm thick glass (inner dimensions 70 × 70 × 70 mm, with removable lid providing access to interior when cleaning). There were two holes in each cube (opposite each other; diameter 20 mm; each centred on a side of the cube) and each was plugged with a rubber stopper. Glass tubes were inserted into each stopper (diameter of hole in stopper 4 mm) and these, along with silicone tubing, bridged airflow throughout the apparatus.

In cryptic trials (figure 1*a*), 'masking odour' was provided by putting cuttings (stems, leaves and flowers) from *Lantana camara* in two masking chambers, one positioned in front of the stimulus chamber and the other in front of the control chamber. The role of the masking odour was to make the source of prey or mate odour more difficult to find, and the rationale for using *L. camara* as a masking odour was previous research (Cross & Jackson 2009*c*) showing that the odour of this plant species is salient to *E. culicivora*. There was also a transition chamber through which the test spider had to pass before getting close to the odour source (figure 1*a*), the rationale again being that this would make it more difficult for the test spider to find the odour source. To make the space inside the transition chamber more complex, there was a glass pillar (height, 70 mm; diameter, 25 mm) positioned in each of its four corners. Preliminary data showed that having the four pillars in a transition chamber increased the difficulty of finding a cryptic odour source. Conspicuous trials were like cryptic trials except for the absence of the masking odour and the transition chamber (figure 1*b*).

A pump coupled to two Matheson FM-1000 flow meters was used for pushing air through the apparatus (airflow 1500 ml min^{-1}). In cryptic trials (figure 1*a*), air moved independently through the stimulus chamber and a masking chamber on one side of the Y and through the control chamber and a masking chamber on the other side of the Y. From the two arms of the Y, air then moved into the test arm and, from there, air moved through a glass corridor (length, 40 mm; diameter, 20 mm) into the transition chamber and then through a holding chamber before exiting through a hole in a stopper. In the conspicuous trials (figure 1*b*), the air path was the same except there was no corridor, transition chamber or masking chamber.

For each trial, whether the stimulus chamber was on the left or on the right side was decided at random. The test spiders' access to the chambers of the Y maze was blocked by nylon netting over the ends of the silicone tubing. Test spiders could not see the contents of the stimulus and masking chambers because an opaque plastic screen was positioned between the Y maze and the chambers. Prey or a mate was put in the stimulus chamber 30 min before trials began and cuttings from *L. camara* (collected 60–90 min beforehand from the field; using a microscope, any visible arthropods removed) were put in the bottom part of each masking chamber (i.e. foliage did not rise above the level of the inflow and outflow holes of the masking chambers).

Before each trial began, the test spider was kept for 10 min inside a holding chamber (figure 1*c*), with this chamber connected by silicone tubing to a priming chamber containing either 20 mosquitoes or one mate. An opaque plastic screen between the holding and the priming chambers hid the odour source from the test spider's view. A pump and one flow meter pushed air through the priming and the holding chambers (airflow, 1500 ml min^{-1}).

When the priming interval finished, the stopper at the end of the holding chamber furthest away from the spider was removed. In conspicuous trials (figure 1*b*), the open end of the holding chamber was inserted into a rubber stopper that covered the entrance to the Y maze. In cryptic trials (figure 1*a*), the open end of the holding chamber was inserted into the transition chamber. A glass corridor (inserted into rubber stopper that covered entrance to Y maze) connected the transition chamber to the Y maze. The spider was free to move into the test arm after leaving the holding chamber (conspicuous trials) or corridor (cryptic trials).

Maximum trial duration was 60 min. If the test spider entered the stimulus arm and remained there for 30 s, the trial ended and the outcome was recorded as the spider having found the experimental odour. The entire apparatus was lit with a 200 W incandescent lamp (positioned 400 mm overhead), with ambient lighting coming from overhead fluorescent lamps. Between trials, the apparatus was dismantled and cleaned with 80 per cent ethanol followed by distilled water, and then dried.

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

odour to find	priming stimulus	test spider	χ^2_1 test of independence
cryptic versus conspicuous mosquito	mosquitoes	male	69.34, $p < 0.001$
		female	86.40, $p < 0.001$
	mates	male	236.89, $p < 0.001$
		female	208.55, $p < 0.001$
	none	male	180.23, $p < 0.001$
		female	176.34, $p < 0.001$
cryptic versus conspicuous mate	mosquitoes	male	251.76, $p < 0.001$
		female	279.24, $p < 0.001$
	mates	male	91.98, $p < 0.001$
		female	104.56, $p < 0.001$
	none	male	183.13, $p < 0.001$
		female	195.65, $p < 0.001$

(c) *Data analysis*

Data were analysed using χ^2-tests of independence, Bonferroni adjustments being applied whenever there was repeated testing of the same datasets ($\alpha = 0.05$, adjusted $\alpha = 0.017$; see Howell 2002). For each condition in cryptic and conspicuous trials, n was always 240 (i.e. 2880 individual males and 2880 individual females were used).

3. RESULTS

(a) *Does the cryptic-conspicuous distinction matter?*

Significantly more spiders found conspicuous odour sources than cryptic odour sources, regardless of whether the spider was primed with congruent odour, primed with incongruent odour or not primed (table 1; figures 2*a*,*b* and 3*a*,*b*). Based on these findings, we are confident that our methods were effective at making odour sources more difficult to find in the cryptic trials and easier to find in the conspicuous trials.

(b) *Does the priming stimulus matter when odour is conspicuous?*

The number of spiders that found the conspicuous odour source after congruent priming (i.e. found mosquito after being primed by smelling mosquitoes, and found mate after being primed by smelling mates) was not significantly different from the number that found the conspicuous odour source after incongruent priming or after no priming. Moreover, the number of spiders that found the conspicuous odour source after incongruent priming was not significantly different from the number that found the conspicuous odour source after not being primed (table 2; figures 2*a*,*b* and 3*a*,*b*).

(c) *Does the priming stimulus matter when odour is cryptic?*

Significantly more spiders found the cryptic odour source after congruent priming than after incongruent priming or after no priming. Moreover, significantly fewer spiders found the cryptic odour source after incongruent priming than after no priming (table 2; figures 2*a*,*b* and 3*a*,*b*).

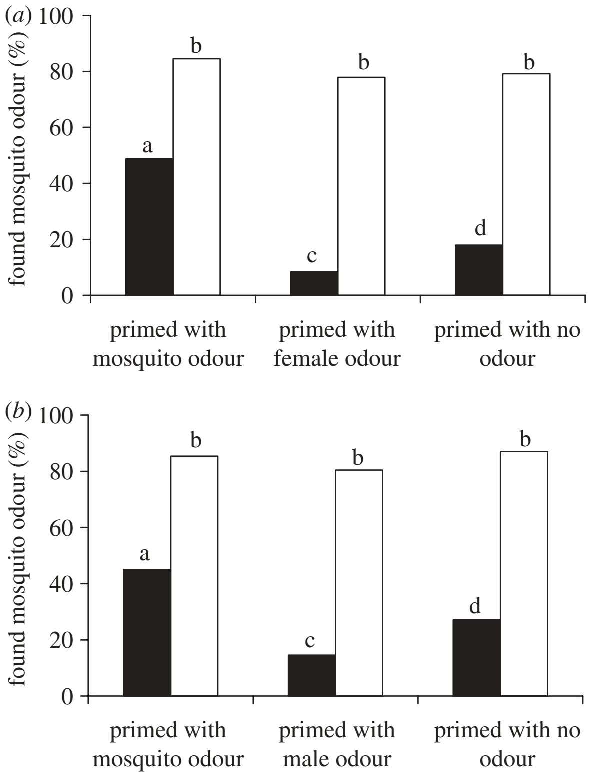

Figure 2. *Evarcha culicivora* (*a*) males and (*b*) females that located source of mosquito odour (cryptic or conspicuous). Spiders primed with odour of mosquitoes, with odour of potential mates or with no odour. Different letters above bars denote significantly different ($p < 0.05$); same letters, not significant ($p > 0.05$). Filled box, cryptic; open box, conspicuous.

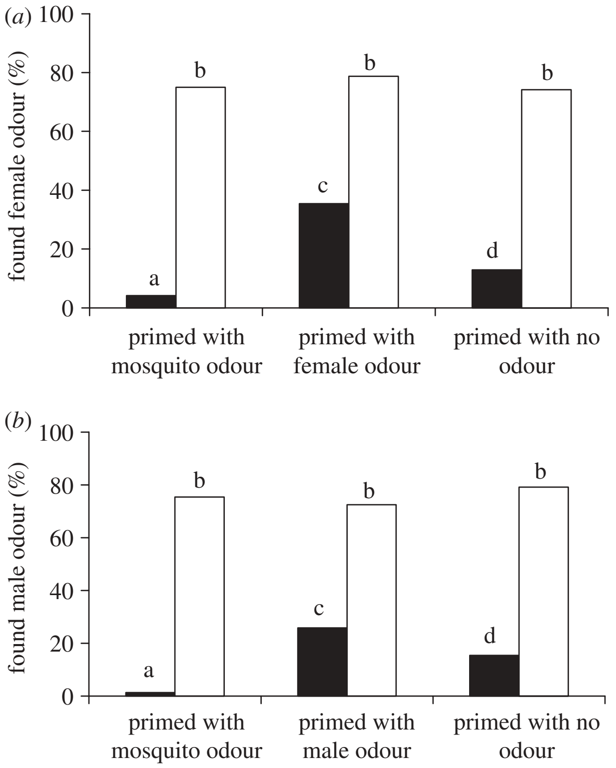

Figure 3. *Evarcha culicivora* (*a*) males and (*b*) females that located source of potential-mate odour (cryptic or conspicuous). Spiders primed with odour of mosquitoes, with odour of potential mates or with no odour. Different letters above bars denote significantly different ($p < 0.05$); same letters, not significant ($p > 0.05$). Filled box, cryptic; open box, conspicuous.

4. DISCUSSION

In our study, *E. culicivora* found the source of a particular odour more readily after prior experience with that odour and, in basic respects, this result is similar to the results in other olfactory search image studies. For example, once skunks have learnt the odour of a particular type of food, they show evidence of detecting this odour in a natural grassy area from greater distances than before learning (Nams 1991, 1997). Another example is sniffer dogs that, after smelling a higher concentration of TNT beforehand, find significantly more containers holding TNT than sniffer dogs that have smelled a lower concentration of TNT (Gazit *et al.* 2005).

Yet, there is an important difference. We compared what happens when odour is conspicuous with what happens when odour is cryptic. The cryptic–conspicuous distinction is critical for determining whether the primary effect of prior experience is a change in preference (motivation) or a change in selective attention (Shettleworth 1998; Cross & Jackson 2006), but this comparison was not explicitly considered in the skunk or in the dog studies (Nams 1991, 1997; Gazit *et al.* 2005). An animal's preferences should be readily expressed when an odour source is easy to find, whereas the influence of selective attention should be most evident when an odour source is hard to find. Our data suggest that we succeeded in making odour sources more difficult to find (cryptic) or easier to find (conspicuous). We also showed that significantly more spiders found an odour after congruent priming than after incongruent priming, but only when the odour source was cryptic. This is the evidence needed for concluding that *E. culicivora* makes use of olfactory search images and ruling out the alternative hypothesis concerned with preference change.

Presenting *E. culicivora* with only one odour source at a time in the Y maze was critically important in our methods because, if *E. culicivora* had been forced to make a choice between two different odour sources, it would have been impossible to determine whether the spider's response of moving into a particular arm of the Y was because it was selectively attentive to the odour in that arm or because it preferred the odour found there. By presenting only one odour source at a time, we examined specifically whether *E. culicivora* was using selective attention. That *E. culicivora* might simply be motivated to move towards a particular odour source is unlikely because there was no significant effect of priming in the conspicuous trials.

In the cryptic trials, besides having become more effective at finding a congruent odour source after priming, *E. culicivora* also became less effective at finding an incongruent odour source after priming. For example, when the task was to find the source of cryptic mate odour, significantly fewer spiders found it after they were primed by smelling mosquitoes rather than after no priming. This suggests that *E. culicivora* has limited capacity for attention and that there are trade-offs, whereby being primed to notice one thing diminishes the capacity to notice something else. Although Tinbergen (1960) suggested that birds might make use of more

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

odour to find	priming stimulus	test spider	χ_1^2 test of independence
conspicuous mosquito	mosquitoes versus mates	male	3.50, $p = 0.061$
		female	2.12, $p = 0.146$
	mosquitoes versus no priming	male	2.37, $p = 0.124$
		female	0.28, $p = 0.596$
	mates versus no priming	male	0.11, $p = 0.739$
		female	3.92, $p = 0.050$
conspicuous mate	mates versus mosquitoes	male	0.95, $p = 0.330$
		female	0.53, $p = 0.467$
	mates versus no priming	male	1.40, $p = 0.237$
		female	2.91, $p = 0.088$
	mosquitoes versus no priming	male	0.04, $p = 0.834$
		female	0.96, $p = 0.327$
cryptic mosquito	mosquitoes versus mates	male	96.11, $p < 0.001$
		female	53.08, $p < 0.001$
	mosquitoes versus no priming	male	51.34, $p < 0.001$
		female	16.71, $p < 0.001$
	mates versus no priming	male	9.67, $p = 0.002$
		female	11.37, $p = 0.001$
cryptic mate	mates versus mosquitoes	male	73.82, $p < 0.001$
		female	61.94, $p < 0.001$
	mates versus no priming	male	33.15, $p < 0.001$
		female	7.95, $p = 0.005$
	mosquitoes versus no priming	male	11.76, $p = 0.001$
		female	31.53, $p < 0.001$

than one search image at any given time, it is now widely appreciated that selective-attention tasks are subject to severe capacity limitations (e.g. Dukas & Kamil 2001) and that being selectively attentive to one target stimulus can interfere with detecting other targets (e.g. Pietrewicz & Kamil 1979). Interference effects are further evidence that selective attention, instead of preference, explains the findings from our search-image experiments.

Interference effects when salticids adopt search images have been shown before with *E. culicivora* (Cross & Jackson 2010) and with *Portia labiata* (Jackson & Li 2004), an araneophagic salticid species from the Philippines, but not specifically in the context of selective olfactory attention. For both of these species, seeing one thing (a prey species or a mate) diminishes the ability to find something else. Another way in which findings in the present study and in the earlier studies are consistent is that, for priming selective attention, a single experience with a particular stimulus sufficed. This is considerably different from conventional search-image studies where training is integral (i.e. it is conventional to envisage search-image acquisition being based on perceptual learning after repeated encounters with a particular type of prey). Yet, in our study, despite test spiders having no opportunity to eat or mate during priming, and despite the only possible reinforcement coming from smelling prey or a mate, test spiders still became selectively attentive to the priming stimulus. This suggests that, instead of being trained to identify prey or mates (i.e. learning), *E. culicivora* called up an innate (pre-existing) search image when primed by prey or mate odour.

Although olfactory search images are not considered as often as visual search images in the literature, our research has shown that both visual (Cross & Jackson 2010) and olfactory search images are important for *E. culicivora* when finding prey and mates. This suggests that, for understanding the role of selective attention in governing animal behaviour, more experimental research on olfactory search images would be rewarding.

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