2015. Journal of Arachnology 43:123–142

REVIEW

Mosquito-terminator spiders and the meaning of predatory specialization

Robert R. Jackson and **Fiona R. Cross**: School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand; International Centre of Insect Physiology and Ecology, Thomas Odhiambo Campus, Mbita Point, Postal Code 40305, Kenya; E-mail: robert.jackson@canterbury.ac.nz

Abstract. Many spiders eat mosquitoes, but a spider is not automatically a mosquito specialist if it eats mosquitoes, or even if it primarily eats mosquitoes. Instead, specialization pertains to predators being adaptively fine tuned to specific types of prey. It is important to keep this basic meaning of specialization conceptually distinct from diet breadth (stenophagy versus euryphagy), adaptive trade-offs and other sister topics. Here we review the biology of *Evarcha culicivora* Wesolowska & Jackson 2003 and *Paracyrba wanlessi* Żabka & Kovac 1996 (Salticidae), two spider species that can be characterized, in their own individual ways, as being mosquito specialists. However, simply calling these species mosquito specialists can be misleading. Details matter, with some of the most important of these details pertaining to the different ways *E. culicivora* and *P. wanlessi* classify mosquitoes. The way these species classify, and specialize on, mosquitoes includes fine-tuned prey-choice behavior, special feature-detection mechanisms, deployment of selective attention and other behavioral and cognitive capacities that can be understood only on the basis of appropriately designed experiments.

Keywords: Preferences, predatory versatility, search images, trade-offs, Salticidae, *Evarcha culicivora*, *Paracyrba wanlessi*

TABLE OF CONTENTS

1. INTRODUCTION

As arachnologists, we like spiders, but we are all too familiar with people who enjoy telling us, often with considerable pride, about their fear and loathing for our favorite animals (see Vetter 2015). Yet even people who dislike spiders often concede that spiders are the lesser of two evils when the alternatives are mosquitoes. Fear of spiders is almost always irrational, but disliking mosquitoes is easier to justify because, besides being a nuisance, mosquitoes are the vectors of some notorious human diseases including dengue, yellow fever and especially malaria (Becker et al. 2010; Godfray 2013). Most people like to hear that spiders eat mosquitoes, but the news that some spiders are actually mosquito specialists, or what we call "mosquito terminators", can seem like a step toward curing even hard-core arachnophobia.

However, therapy for arachnophobia is not what we are about. Our primary interest is in what mosquito terminators can tell us about predatory specialization. When we use the term "specialization", we mean that a predator is especially well adapted with respect to specific types of prey. We emphasize this because, regardless of whether we are talking to non-specialists (e.g., the lay public) or to specialists (e.g., ecologists who spend a lot of time thinking and writing about specialization), we know all too well that the term "specialization" can trigger a lot of confusing, contradictory notions. This problem is not something to dismiss by saying it is just semantics.

For example, many reports in the literature may be cited as evidence that spiders can and do eat adult mosquitoes (Mathis & Berland 1933; Ramoska & Sweet 1981; Nandi & Raut 1985;

Figure 1.—Adult male of *Evarcha culicivora* preying on *Anopheles gambiae s.s.* Photograph: Robert Jackson

Figure 2.—Adult male of *Paracyrba wanlessi*. Photograph: Daiqin Li.

Sulaiman et al. 1990, 1996; Strickman et al. 1997; Maimusa et al. 2012; Weterings et al. 2014) and the aquatic juveniles of mosquitoes (Bishop & Hart 1931; Garcia & Schlinger 1972; Service 1973; Greenstone 1979, 1983; Breene et al. 1988; Perevozkin et al. 2004; Futami et al. 2008). However, the objectives, methods and types of data vary substantially from study to study. Moreover, it is rare to find details and robust, evidence-based conclusions about spiders specializing at preying on mosquitoes.

When discussing predatory specialization, we need an in-depth understanding of how particular predators are adaptively fine tuned to specific types of prey. For this, relying solely on field sampling or solely on observations will not suffice. Well-designed experiments are essential. *Evarcha culicivora* Wesolowska & Jackson 2003 from the Lake Victoria region of East Africa (Wesolowska & Jackson 2003) and *Paracyrba wanlessi* Żabka & Kovac 1996 from Peninsular Malaysia (Żabka & Kovac 1996) are the only two mosquito-eating spider species that can currently, on the basis of extensive experimental evidence, be characterized as mosquito specialists. These two species (Figs. 1 & 2) specialize on mosquitoes in strikingly different ways and they come from very different habitats, with *E. culicivora* most often being found on walls of buildings occupied by people and *P. wanlessi* most often being found in the culms of bamboo. However, from a practical perspective, these two species have something important in common. They are both jumping spiders (Salticidae).

Using their unique, complex eyes, salticids see with a level of spatial resolution unparalleled by other animals of comparable size (Harland et al. 2012; Land & Nilsson 2012) and, among salticids, we find some of the most intricate vision-guided predatory strategies in the animal kingdom (Gardner 1964; Forster 1982; Jackson & Pollard 1996). Their visual capacities make salticids especially suitable experimental subjects for research on predatory specialization. For example, salticids readily respond to lures made by mounting dead prey in life-like posture on cork discs (Jackson & Tarsitano 1993) and to virtual prey generated by computer 3D animation software (Harland & Jackson 2002; Nelson & Jackson 2006; Dolev & Nelson 2014). This is important because it means potentially confounding variables that arise when using living prey can be readily removed from experiments when using salticids as the predators (Jackson & Cross 2011).

Besides standardizing the stimuli that we present to a test spider in an experiment, we need to minimize any potential confounding effects pertaining to the test spiders themselves. In our laboratories in New Zealand and Kenya, we rear salticids in very large numbers and often we use thousands of these spiders in a single publication. This is important when we need to draw robust conclusions that take into account the range of factors that can introduce variability into data on behavior. For example, repeatedly testing the same individual introduces prior experience as a potentially important confounding variable, along with raising issues pertaining to pseudoreplication. However, we routinely minimize these problems by only using each individual salticid in a single trial. We also standardize test-spider sex, age and body size, prior feeding, prior mating, prior egg-laying and a host of other factors pertaining to rearing and maintenance. These exacting features of our methods all require especially large numbers of spiders. Large sample sizes also become important for statistical power when we use individual data sets in multiple comparisons for asking different questions. We also continue to develop new experimental protocols and apparatus, which is important because, when we find converging evidence from a variety of experiments, this increases confidence in our conclusions.

We emphasize details about methods when discussing mosquito terminators for two reasons. One is to dispel any false impression that it is easy to determine a predator's preferences, prey-choice behavior, reliance on search images and various other characteristics related to specialization. The other is that details pertaining to methods are not just incidental information. On the contrary, understanding the methods is critical for understanding what specialization actually means.

2. SPECIALIZATION, PREFERENCE AND PREY-CHOICE BEHAVIOR

In the literature on ecology and evolutionary biology, predators are often called "specialists" and "generalists" on the basis of whether their natural diets are "narrow" or "wide" (Futuyma & Moreno 1988; Wise 1993; Berenbaum 1996), but this is a major source of confusion because "specialization" is precisely the term we need for something else. "Monophagy", "oligophagy", "polyphagy", "stenophagy" and "euryphagy" are terms that pertain to the breadth of a predator's natural diet, but "specialization" is the specific term we need when discussing the characteristics that make a predator especially proficient at targeting a particular type of prey. Using "specialization" and "specialist" in the context of diet breadth, instead of strictly in the context of adaptive fine tuning, blurs critically important conceptual distinctions, making it easy to misconstrue data related to diet breadth as being evidence of adaptations that make a predator especially proficient at targeting particular prey types.

Tempting though it may be, it is not good enough in this instance simply to say that different people use different definitions for the same words. Nor are we suggesting that the term "specialization" is too vague to be useful. Being vague is not the problem, but we do need to be clear about the context in which "specialization" is the appropriate term to use, and specifying the context is not so especially difficult.

For example, Pekár & Toft (in press) proposed that we should distinguish between the "evolutionary context" and the "ecological context", these being terms for two conceptually distinct contexts in which predators can be discussed. In the evolutionary context, "specialization", "specialist" and "generalist" are appropriate terms for what Pekár and Toft (in press) call "degree of adaptation". In this context, the proper focus is on how the predator's phenotype is adapted to targeting a specific kind of prey. However, in the ecological context, when predators are considered in terms of the breadth of their natural diets, the appropriate terms are "stenophagy" and "euryphagy", not "specialization", "specialist" and "generalist". Ideas about niche construction (Laland et al. 1996) notwithstanding, we need to acknowledge that natural diet is often influenced by other variables, such as prey availability and a prey species' defensive behavior, that are not strictly a part of the predator's phenotype.

It is especially confusing when the terms "choice" and "preference" are used in the ecological context because we need these terms for discussing behavior, motivation and cognition in the evolutionary context. There are other expressions, such as "selection of prey" and "bias in diet toward" that make more sense in the ecological context. At best, data related to natural diet, including any deviations between diet and available prey in a particular habitat, might be a rationale for hypotheses about choice and preference (Jackson & Cross 2011). However, evaluating these hypotheses requires data from experiments that are specifically designed for investigating decision making and motivation (e.g., Huseynov et al. 2008). In casual language, we can say an animal's preference is what it would like to eat, which is good because it reminds us that an animal's natural diet (what it actually does eat) might be different from its preferences ("you can't always get what you want").

In the ecological context, we know that the natural diets of *E. culicivora* and *P. wanlessi* are biased toward mosquitoes, and we also know that *E. culicivora* and *P. wanlessi* eat other prey in the field (Zabka & Kovac 1996; Wesolowska & Jackson 2003). We acknowledge that it would be useful to have a more thorough understanding of these spiders' natural diets and of where these two species can be placed on a stenophagy-euryphagy continuum. However, details from the ecological context will not answer questions about specialization and, in most of the research on mosquito terminators, it is the evolutionary, and not the ecological, context that has been the major focus.

3. THE PREFERENCE PROFILE OF *EVARCHA CULICIVORA*

Finding a predator with an active preference for mosquitoes is strikingly unusual, but *E. culicivora* takes "unusual" to another level (Cross & Jackson 2010a). The females of most mosquitoes feed on vertebrate blood (Clements 1992), and *E. culicivora* also feeds on vertebrate blood, but indirectly. Many arthropods, including female mosquitoes, use specialized mouthparts for piercing vertebrate skin and ingesting blood (Lehane 2005), but spider mouthparts are not specialized in the same way (Foelix 2011). The way *E. culicivora* gets a blood meal is by expressing a preference for the female mosquitoes that are carrying blood from their own recent blood meals.

The closest parallel to *E. culicivora*'s strategy might be an ectoparasite instead of another predator. *Culicoides anophelis* Edwards is a midge that feeds on vertebrate blood. It can take its blood meals directly from cattle and from other mammals. However, like a tick on a cow, this minute midge is sometimes found attached to a blood-carrying mosquito. In these instances, like *E. culicivora*, *C. anophelis* apparently feeds indirectly on vertebrate blood by taking the blood from a mosquito (Edwards 1922; Laird 1947; Chu 1959; Chhilar & Chaudhry 2010; Ma et al. 2013). Being an ectoparasite instead of a predator, perhaps this midge should not be called a mosquito terminator, but it would be interesting to carry out experiments aimed at determining whether *C. anophelis*, like *E. culicivora*, is a specialist at taking indirect blood meals from mosquitoes.

Among salticids, distinctive vision-based prey-choice behavior has been documented especially for species that specialize at eating ants and species that specialize at eating other spiders (Nelson & Jackson 2011; Cushing 2012; Jackson & Nelson 2012a). Ants and spiders as prey can be particularly dangerous for a salticid and it has been suggested that this element of risk has, as a selection factor, favored an especially intricate expression of predatory specialization (Jackson 1992; Jackson & Cross 2013). However, mosquitoes are not particularly dangerous and yet the level of specificity shown by *E. culicivora* is exceptional (Table 1). Moreover, *E. culicivora* is one of the few salticids (Jackson et al. 2002; Cerveira & Jackson 2011) known to be proficient at identifying preferred prey even when restricted to using olfaction alone (Jackson et al. 2005).

Evarcha culicivora's habitat teems with insect life, including chironomid and chaoborid midges. These midges, known locally as "lake flies", often arrive on Lake Victoria's shoreline in enormous swarms that blanket houses, choke the vegetation and blacken the sky (Carpenter 1920; Beadle 1981). Although lake flies, which resemble mosquitoes in general body form and size, vastly outnumber the mosquitoes, *E. culicivora* has most often been observed in the field feeding on mosquitoes

Table 1.—Two mosquito-terminator salticids compared.

	Evarcha culicivora	*Paracyrba wanlessi*
Locality	Western Kenya	Peninsular Malaysia
Habitat	Walls of buildings	Culms of bamboo
Adult mosquitoes (terrestrial prey) dominant in natural diet	Yes	Yes
Juvenile mosquitoes (aquatic prey) dominant in natural diet	No	Yes
Chooses adult mosquitoes in preference to other terrestrial prey	Yes	Yes
Chooses blood-carrying mosquitoes in preference to non-blood-carrying prey	Yes	No
Chooses adult female mosquitoes in preference to adult male mosquitoes even in absence of blood	Yes	No
Chooses adult anopheline mosquitoes in preference to adult non-anopheline mosquitoes even in absence of blood	Yes	No
Chooses juvenile mosquitoes in preference to other aquatic prey	NA	Yes
Chooses non-mosquito prey in water in preference to non-mosquito prey away from water	NA	Yes
Chooses juvenile mosquitoes in water in preference to juvenile mosquitoes away from water	NA	Yes
Chooses adult mosquitoes away from water in preference to non-mosquito prey in water	NA	Yes
Chooses adult mosquitoes in water in preference to non-mosquito prey in water	NA	Yes
Chooses adult mosquitoes in water in preference to adult mosquitoes away from water	NA	Yes
A versatile predator that deploys different prey-capture methods with different types of prey	Yes	Yes

(Fig. 1) instead of on lake flies, and the mosquitoes being eaten by *E. culicivora* have especially often been species from the genus *Anopheles* (Wesolowska & Jackson 2003). These field data suggested hypotheses about preferences (i.e., that *E. culicivora* expresses a preference for mosquitoes instead of non-mosquito prey, for blood-carrying instead of non-blood-carrying mosquitoes and for *Anopheles* instead of other mosquito genera) and these hypotheses have now been corroborated by findings from experiments (Jackson et al. 2005; Nelson & Jackson 2006).

However, for characterizing *E. culicivora*'s predatory strategy, we need to think about preference profiles instead of simply specifying a preferred prey category. Among other things, preference profiles need to take into account adult-juvenile differences in the expression of preferences and the effects of hunger level on prey-choice behavior. Much of what we know about *E. culicivora*'s innate preference profile comes from what is currently the most comprehensive experimental study available on any salticid's vision-based prey-choice behavior (Nelson & Jackson 2012a). In these experiments, *E. culicivora* chose lures that had been made from both sexes of two mosquito species, *Culex quiquefasciatus* Say and *Anopheles gambiae s.s.* Giles, in preference to lures made from a lake fly, *Clinotanypus claripennis* Kieffer (Chironomidae).

The objective was to determine, for *E. culicivora*, the preference profile that was innate (Nelson & Jackson 2012a). This meant that, besides minimizing the possibility of individual learning, the methods also minimized the possibility that maternal effects (Mousseau & Fox 1998) might be confounding variables. For example, no test spiders and no test spider's parents had prior encounters with the apparatus, the testing procedures or the types of prey used in experiments, and no individual was used more than once as a test spider.

The mosquitoes came from cultures maintained on a 6% glucose solution (Mukabana et al. 2002) and, for both mosquito species, two types of females were used (Nelson & Jackson 2012a). Blood-carrying females fed on blood and then, 4 h later, they were used for making lures. No-blood females received only the standard sugar maintenance diet. When making a lure (see Jackson et al. 2005), a living prey item was first immobilized with carbon dioxide and then immersed in ethanol. When removed from the ethanol the next day, the prey item was positioned in lifelike posture on a thin cork disc, with the diameter of the disc being similar to the body length of the prey item. For preservation and for retaining the prey's normal resting posture, the lure was then sprayed with a clear aerosol plastic adhesive. No lure was used in more than one experiment or more than once in a single experiment (Nelson & Jackson 2012a).

For ascertaining the influence of hunger level on the expression of preferences, each test spider was fed to satiation and then, before being used in a trial, it was held without prey for 1, 7, 15 or 21 days (Nelson & Jackson 2012a). The testing apparatus was a transparent glass arena sitting on a plastic platform (Fig. 3). Each trial began when a spider was introduced through a hole in the glass floor of the arena. This hole was close to one end of the arena. For displaying lures, there were three holes (left hole, right hole & center hole) outside the opposite end of the arena. The spider could see, but not contact, the lures from inside the arena.

Three testing protocols were adopted (Nelson & Jackson 2012a). In simultaneous-presentation tests, *E. culicivora* was exposed to two lures at the same time, each lure being made from a different kind of prey. One lure was centred on top of the left hole and the other lure was centred on top of the right hole. In alternate-day and alternative-prey tests, a single lure was centred on top of the central hole, and these tests were carried out over two trials on successive days. In alternate-day tests, *E. culicivora* was exposed to a single lure of one type on one day and a single lure of another type on the next day. The prey type presented first was decided at random and only those test pairs in which *E. culicivora* chose one prey, but not the other, were used as data for determining preference. In alternative-prey tests, the spider was exposed to a single lure made from one prey type while it was feeding on another prey type. The prey type that the spider ate on the first day was used as a lure on the second day.

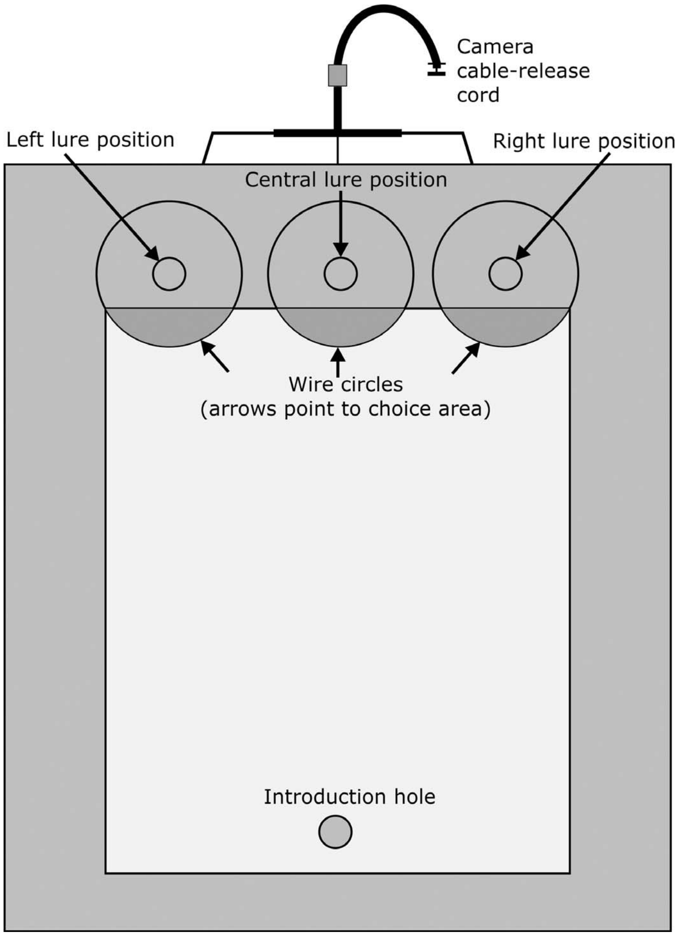

Figure 3.—Prey-choice apparatus (top view) used for determining the preference profile of *Evarcha culicivora*. Rectangular glass box (light gray rectangle in figure) with glass lid, sitting on top of Plexiglas stand (dark gray rectangle). Movement of lures controlled by using a camera release cord. ‘Choice area’: dark gray semicircular area within wire circles. Left and right lure positions used in simultaneous-presentation tests. Central lure position used in alternate-day and alternative-prey tests. From Nelson and Jackson (2012a).

For all three testing protocols, each lure was positioned so that it faced the arena and it stayed in place because the diameter of the hole was narrower than the diameter of the cork disc (Nelson & Jackson 2012a). Although many salticids, including *E. culicivora*, are known to respond to quiescent prey and stationary lures (Harland et al. 2012), moving stimuli are more effective at eliciting predatory responses (Zurek et al. 2010) and, for this reason, the apparatus was designed so that the lures could be moved in a standardized way. A metal prong attached to a camera cable-release cord was connected to the underside of each of the two cork discs in simultaneous-presentation tests and to the single cork disc in alternate-day and alternative-prey tests. Pressing the cable-release moved each lure 5 mm above the floor of the arena and then, by releasing the cable, each lure moved back to the floor. Starting when the test spider entered the arena, the cable-release was pressed once every 30 s.

Circles made from thin copper wire were placed on the platform and a hole for a lure was situated at the center of each circle (Nelson & Jackson 2012a). The circles extended under the arena and they were visible because the bottom of the arena was transparent. There were two circles (one around the left hole and one around the right hole) during simultaneous-presentation testing and there was one circle (around the center hole) during alternate-day and alternative-prey testing. The part of the arena above the wire circle was the “choice area”. The operational definition of “choice” was the test spider fixating its gaze on a lure and then entering the choice area. “Fixate” refers to the corneal lenses of the salticid’s large forward-facing principal eyes being held oriented toward a lure (Land 1971).

Each simultaneous-presentation test and each alternate-day test began when the test spider entered the arena. Alternative-prey tests were more complicated to initiate. First, the test spider was put in a Petri dish with a single prey item. After capturing and beginning to feed on this prey item, the test spider was introduced into the arena while it was still feeding. The operational definition of “choice” in alternative-prey testing included, as an additional requirement, that the spider had to drop the prey on which it was feeding, either before entering or while inside the choice area (i.e., only spiders that dropped their prey were used for analysis).

Evarcha culicivora always expressed weaker preferences after longer fasts (Nelson & Jackson 2012a). However, hunger-induced weakening of preference was most pronounced during alternative-prey testing, least pronounced during simultaneous-presentation testing and intermediate during alternate-day testing. Juveniles as well as adults preferred blood meals, but adults expressed this preference more strongly than juveniles. Regardless of testing method, when one prey was a blood-carrying female mosquito and the other prey was not carrying blood (i.e., the other prey was a no-blood female mosquito, a male mosquito or a lake fly), adults expressed a strong preference for the blood meals. When both mosquitoes were carrying blood and when both mosquitoes were not carrying blood, adults and juveniles of *E. culicivora* chose *Anopheles* in preference to *Culex*. However, when presented with *Culex* carrying blood and *Anopheles* without blood, adults chose the blood meal (i.e., *Culex*) but juveniles chose *Anopheles*, the no-blood meal. These findings show that preference for *Anopheles* is expressed by juveniles more strongly than by adults, whereas preference for blood meals is expressed by adults more strongly than by juveniles. The findings from these experiments also revealed that, independent of blood meals, juveniles and adults choose female mosquitoes in preference to male mosquitoes.

Some progress has been made toward understanding the prey-identification cues that matter to *E. culicivora*. For example, anopheline mosquitoes adopt a characteristic resting posture with their abdomens tilted up, whereas resting non-anopheline mosquitoes hold their bodies horizontal (Clements 1999). In experiments using lures and computer-generated virtual mosquitoes projected onto miniature screens, *E. culicivora* expressed a preference for the abdomen-tilted-up posture (Nelson & Jackson 2006). Later work showed that the relative angles between mosquito body parts, instead of the angle of the body to surface or horizon, are the critical cues (Dolev & Nelson 2014). However, when discriminating between male and female mosquitoes, *E. culicivora* attends to male-

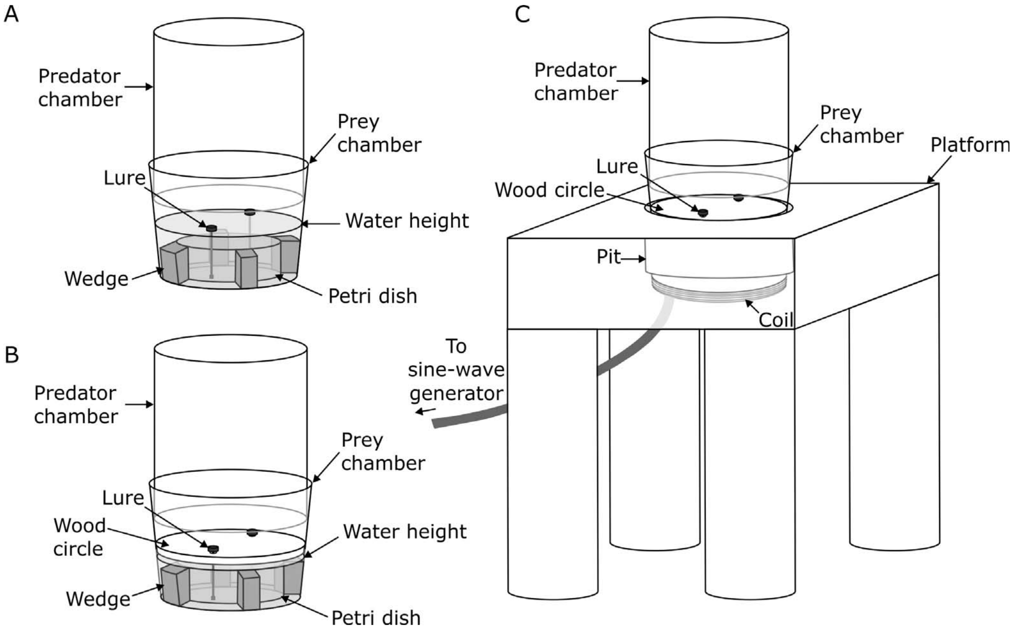

Figure 4.—Prey-choice apparatus used for determining the preference profile of *Paracyrba wanlessi*. A. When lures were in water. B. When lures were away from water. Start of test: test spider in predator chamber and walks down to prey chamber. C. Prey chamber sat inside a pit on top of a wooden platform. Two lures were present at any one time, and lures were moved during the test by using a sine-wave generator connected to a coil situated underneath the platform (held with a plastic stand; not shown). End of test: test spider attacks lure. From Jackson et al. (2014).

female differences in the appearance of the mosquitoes' antennae (Nelson & Jackson 2012b).

4. THE PREFERENCE PROFILE OF *PARACYRBA WANLESSI*

Like *E. culicivora*, *P. wanlessi* (Fig. 2) has a strong preference for mosquitoes as prey (Jackson et al. 2014) and yet *E. culicivora* and *P. wanlessi* have distinctively different preference profiles. When people speak of mosquitoes in casual conversation, it is often understood that they mean adult mosquitoes and it is as though *E. culicivora* agrees since this predator is known to target only the adult stages of the mosquito. *Paracyrba wanlessi* is different (Table 1) because it has a specialized predatory strategy by which it targets juvenile as well as adult mosquitoes. As holometabalous insects, mosquitoes progress during their life cycles from egg to larva to pupa and then to adult. These mosquito stages differ strikingly in appearance and they live in very different habitats, with adults being terrestrial insects that fly about in the environment and juveniles being flightless and aquatic (Clements 1992).

Evarcha culicivora and *P. wanlessi* also live in rather different habitats, and these different habitats make sense in the context of the different prey they target. *Evarcha culicivora* is often found in and around houses inhabited by people (Wesolowska & Jackson 2003), which puts this spider in close proximity to the adult mosquitoes that go to houses in search of blood meals (Clements 1999). *Paracyrba wanlessi*, on the other hand, lives in the hollow internodes (culms) of bamboo (Kovac & Streit 1996; Żabka & Kovac 1996) and, in this habitat, *P. wanlessi* is usually in close proximity to juvenile mosquitoes as well as adult mosquitoes. Water and light enter the bamboo culms through holes made by insects and decay, and mosquitoes lay their eggs in the phytotelmata (i.e., small bodies of accumulated rainwater).

We soon discovered that, for investigating *P. wanlessi*'s preferences, we could not simply rely on the same experimental methods that were used for investigating *E. culicivora*. Slow, frustrating preliminary work eventually gave us apparatus (Fig. 4) and experimental protocols suitable for investigating *P. wanlessi*'s preferences. This was followed by a 7-year period during which thousands of spiders were used in the experiments for characterizing *P. wanlessi*'s preference profile.

For *P. wanlessi* (Jackson et al. 2014), experiments were based on modifying simultaneous-presentation and alternate-day testing protocols used in research on *E. culicivora* (Nelson & Jackson 2012a) and there were comparable controls for prior experience and maternal effects. At the beginning of each trial, the test spider stood at the top of the apparatus, quiescent and facing down. From this position, the test spider could see lures at the bottom of the apparatus and, depending on the experiment, the lures were either in water or away from water. These lures were made from a wide assortment of terrestrial and aquatic arthropods that included, besides mosquitoes (Diptera, Culicidae), other dipterans (Chaoboridae, Chironomidae, Tephritidae) as well as ephemeropterans (Baetidae), heteropterans (Corixidae, Gerridae, Mesovelidae, Miridae, Naucoridae, Notonectidae), lepidopterans (Pyralidae), orthopterans (Gryllidae) and spiders (Araneae: Hersiliidae, Lycosidae, Nephilidae, Salticidae, Theridiidae).

Each lure was a prey individual positioned in lifelike posture on a cork disc, but some of the lures made from aquatic insects required especially painstaking assembly (Fig. 5). For example, a thin metal wire was used for

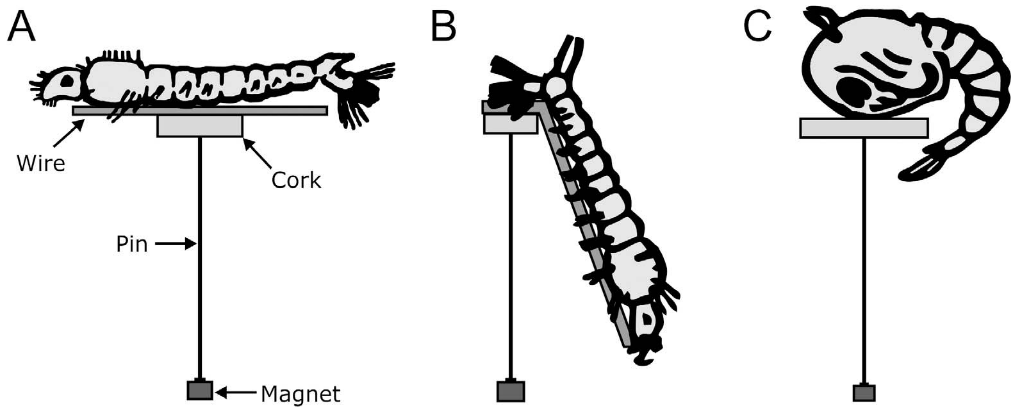

Figure 5.—Lures made from the larvae and pupae of mosquitoes, showing how these prey types were mounted on cork discs for use in experiments designed for determining the preference profile of *Paracyrba wanlessi*. A. *Anopheles* larva, mounted ventral side up, with head rotated 180°. B. *Culex* larva, mounted in a head-down, almost-vertical posture, with the ventral surface of the larva's last abdominal segment on the top of the cork disc. C. *Culex* pupa, mounted with the anterior ventral surface on top of the cork disc. From Jackson et al. (2014).

maintaining the normal posture of the especially slender and soft-bodied prey (caterpillars, beetle larvae & mosquito larvae). The caterpillars, beetle larvae and *Anopheles* larvae were horizontally positioned on the top of the cork discs, with each disc being centred midway along the length of the insect's extended body (see Fig. 5A). Notonectid nymphs and *Anopheles* larvae were mounted ventral side up, as this is the normal resting posture of these insects, but all other prey items were mounted dorsal side up. Moreover, while feeding at the surface of the water, *Anopheles* larvae normally rotate their heads 180° with the rest of their bodies being upside down (Clements 1999). This means the larva's head is dorsal side up, despite its body being upside down, and we simulated this posture when making lures from *Anopheles* larvae.

Culex larvae differ from *Anopheles* larvae by resting head-down in an almost-vertical posture (Fig. 5B). When in this posture, siphons at the posterior end of the *Culex* larva's abdomen are elevated higher than the rest of the body. This posture was simulated by positioning the ventral surface of the *Culex* larva's last abdominal segment on top of the cork disc and aligning the larva's body along a metal wire, with the metal wire extending down from the disc at an angle of 20°.

Mosquito pupae rest in a characteristic posture with the dorsal surface of the cephalothorax above and the rest of the body arched down and under. We replicated this posture by positioning the anterior ventral surface of the pupa on the top of a cork disc (Fig. 5C), with the abdomen curling down and beneath the disc.

Using a coil-and-magnet system, we moved the lures in a standardized way. A trial ended when the spider attacked a lure within 30 min. Otherwise the outcome was recorded as no response. Findings from these experiments showed that, besides expressing a strong preference for adult mosquitoes when lures were away from water, *P. wanlessi* expressed a strong preference for mosquito larvae and mosquito pupae when the lures were in water. Moreover, when presented with adult mosquitoes away from water, *P. wanlessi* differed from *E. culicivora* by showing no evidence of discriminating between male and female mosquitoes, between female mosquitoes carrying blood and female mosquitoes not carrying blood, or between *Anopheles* and non-anopheline mosquitoes.

When the lures were in water, *P. wanlessi* again expressed a strong preference for adult mosquitoes as long as the alternative prey was not a mosquito larva or pupa (i.e., as long as it was not a juvenile mosquito). However, when one of the lures in water was a juvenile mosquito, *P. wanlessi* chose this prey in preference to any other aquatic insects and in preference to adult mosquitoes in water. However, there was no evidence of *P. wanlessi* discriminating between mosquito larvae and mosquito pupae, or between the juveniles of *Anopheles* and the juveniles of non-anopheline mosquitoes.

We also considered the question of whether *P. wanlessi* prefers terrestrial mosquitoes (i.e., adults) or aquatic mosquitoes (i.e., larvae and pupae), but saying simply that *P. wanlessi* prefers one or the other is an unsatisfactory answer because *P. wanlessi* apparently attends simultaneously to mosquito stage (adult versus juvenile) and to mosquito location (away from water versus in water). One of the most interesting findings was that *P. wanlessi* usually expressed a preference for mosquito stages in their normal location (Table 1).

Alternate-day testing was used for investigating whether *P. wanlessi* prefers predatory sequences with prey in water or with prey away from water. This was done by presenting *P. wanlessi* with lures in water on one day and with lures away from water on the next or previous day (sequence determined at random). Some of the findings let us say that *P. wanlessi* prefers attacking prey in water. For example, *P. wanlessi* chose aquatic mosquitoes in water significantly more often than terrestrial mosquitoes away from water. Moreover, when both prey were mosquito larvae or when both were mosquito adults, *P. wanlessi* chose the prey that was in water significantly more often than the prey that was away from water, despite adult mosquitoes in water being in an incongruent location. *Paracyrba wanlessi* also chose adult mosquitoes in water significantly more than non-mosquito prey away from water. However, *P. wanlessi* did not always prefer its prey in water. When the choice was between adult mosquitoes away from water and non-mosquito prey in water, significantly more *P. wanlessi* individuals chose the mosquitoes (Table 1). In other words, prey-type preference was dominant to location preference.

Seeing that prey type and prey location both mattered to *P. wanlessi*, we used a wide variety of feeding regimes for investigating whether prior diet influenced *P. wanlessi*'s preferences and, in each instance, there was no evident effect. For example, *P. wanlessi* individuals expressed the same, apparently innate, preferences regardless of whether or not they had any prior experience with mosquitoes. Perhaps the most remarkable findings were from individuals kept on a diet consisting solely of terrestrial prey, with mosquitoes excluded. Despite having no prior experience with any aquatic prey, these individuals still expressed a preference for juvenile mosquitoes.

The way *P. wanlessi*'s prey-choice behavior differs from *E. culicivora*'s prey-choice behavior illustrates that the details really matter. We can say that both of these salticids are mosquito specialists, but saying no more than that would be seriously misleading. The differences between *P. wanlessi* and *E. culicivora* illustrate why we are wary of simple answers to questions about what a predator prefers eating.

5. PREDATORY VERSATILITY AND PREY-SPECIFIC PREY-CAPTURE BEHAVIOR

"Predatory versatility" (Curio 1976) is a convenient term when discussing predators that deploy conditional predatory strategies and, for the animal kingdom as a whole, some of the most distinctive examples of predatory versatility have come from research on salticids and especially from research on species from the salticid genus *Portia* Karsch 1878 (Harland & Jackson 2004; Jackson & Cross 2013). *Portia* species are not mosquito terminators, as their preferred prey are other spiders (Jackson & Cross 2011). However, it is useful to pause and consider *Portia* because some of the conceptual distinctions that matter for understanding *E. culicivora* and *P. wanlessi* stand out even more emphatically in *Portia*'s predatory strategy (Harland et al. 2012).

We can start with the question of whether *Portia* is a web-building spider or a hunting spider, with web builders normally being envisaged as species that capture prey in their webs and with hunting spiders normally being envisaged as species that capture prey without making use of a web (Foelix 2011). *Portia* does both, and more. Sometimes *Portia* captures prey in its self-built web, but *Portia* will also go on predatory forays and capture prey without making use of a web. Alternatively, *Portia* may invade the webs of other spiders where it preys on the resident spiders, on the resident spider's eggs or on other arthropods in the other spider's web, including ensnared insects and kleptoparasite spider species. Each *Portia* individual also deploys a large repertoire of distinctly different innate prey-specific prey-capture tactics, each of these tactics being an example of specialization on a different prey type. Predatory repertoires differ depending on whether a *Portia* individual is in its own web, in another spider's web or away from webs altogether, and each *Portia* individual can switch rapidly from one innate prey-specific tactic to another and also switch rapidly from using its own web to invading other spiders' webs. It can also switch rapidly to being a predator that captures prey while completely away from webs (Harland & Jackson 2004; Jackson & Cross 2013).

With *Portia*'s repertoire of innate prey-specific prey-capture behavior, we see predatory specialization, and then we see it again and again because, in each *Portia* individual's large repertoire of tactics, distinctly different tactics are adaptively fine tuned in different ways to distinctively different types of prey. With one tactic, *Portia* becomes especially proficient at targeting one prey type. With another tactic, *Portia* becomes especially proficient targeting a different prey type, and on and on. In different ways, *Portia* is a specialist on each different prey type for which it has an innate prey-specific prey-capture tactic.

Being an extreme polyspecialist (West-Eberhard 2003), *Portia* illustrates that the meaning of "predatory specialization" has to go beyond monospecialization and include polyspecialization as well. Saying "specialist" when actually meaning something else (e.g., "monophagy" or "limited to") might go unnoticed when discussing monospecialists. However, thinking about polyspecialists can be a helpful source of dissonance because the occurrence of polyspecialization seems to defy any notion of monophagy and limitations being part of the meaning of "specialization".

Portia is extreme, but mosquito terminators are also polyspecialists. For example, *P. wanlessi* initiates encounters with prey in water by fixating its gaze on a prey item in water from as far as 100 mm away and then, by suddenly stepping forward a few millimetres, pausing for several seconds, stepping forward again and so forth, *P. wanlessi* moves closer to the water (Jackson et al. 2014). If the prey item is especially active, *P. wanlessi* often runs sideways while staying close to the prey at the water's edge, but eventually *P. wanlessi* adopts a distinctive pre-strike posture (body lowered, rearmost legs (legs IV) oriented backward, other six legs (legs I-III) oriented forward). While in this posture, *P. wanlessi* eases forward until touching or almost touching the water. If the prey is now more or less stationary, *P. wanlessi* settles close by and then, after a pause lasting a few seconds to several minutes, suddenly attacks by extending legs I–III over the prey. If the prey is particularly active when *P. wanlessi* settles near the water surface, *P. wanlessi* remains quiescent and later, when the prey comes near, makes a sudden ambushing attack.

When away from water, *P. wanlessi* usually holds on after attacking prey. However, when the prey is in water, *P. wanlessi* often attacks and then fails to hold on. When this happens, *P. wanlessi* repeats the sequence and sometimes success comes only after repeating the sequence dozens of times. Details of *P. wanlessi*'s behavior and decisions are different depending on whether we are considering encounters with prey in or away from water. *Paracyrba wanlessi* is a specialist at preying on juvenile mosquitoes encountered in water and also, in a different way, a specialist at preying on adult mosquitoes encountered away from water.

Evarcha culicivora is also a specialist at preying on adult mosquitoes encountered away from water, but in a different way. Salticid secondary eyes and the peripheral regions of their large forward-facing principal eyes are especially good movement detectors (Land 1969a, 1969b, 1971; Zurek & Nelson 2012), but many salticids are also proficient at detecting and identifying quiescent prey (Harland et al. 2012). Proficiency at detecting and identifying quiescent prey might be especially important for *E. culicivora*, a predator that specializes at preying on blood-carrying mosquitoes because, when these mosquitoes are digesting their blood meals, they tend to sit motionless in secluded locations (Clements 1999). After seeing a quiescent blood-carrying mosquito, *E. culicivora* usually moves slowly to within less than a body length away and then it attacks by lunging forward instead of by leaping (Nelson et al. 2005).

The adults and larger juveniles of *E. culicivora* (typical body length 4–6 mm) usually have no trouble holding on when they attack mosquitoes (typical body length 4–5 mm) regardless of the direction in which the mosquitoes are facing during the predatory sequence. For smaller *E. culicivora* juveniles (body length 1.5–2.0 mm), subduing a mosquito can be more challenging because mosquitoes can shake them off. Being shaken off is especially common when the mosquito, after being attacked head on by the small juvenile, takes off and begins flying. However, the predatory repertoire of small *E. culicivora* juveniles includes an *Anopheles*-specific prey-capture method (Nelson et al. 2005).

After seeing a mosquito in the *Anopheles*-specific rest posture (abdomen tilted up), a small *E. culicivora* juvenile's response depends on spider-to-mosquito orientation (Nelson et al. 2005). If the predatory sequence begins while facing *Anopheles*' rear end, the *E. culicivora* juvenile usually moves directly toward its prey, but the sequence is more interesting when it begins while the *E. culicivora* juvenile is facing *Anopheles* from the front or the side. In these instances, the *E. culicivora* juvenile usually takes a detour (i.e., an indirect path) that brings it to the rear of the mosquito and then, from the rear, the juvenile moves slowly under the mosquito's raised abdomen. Owing to *Anopheles*' raised-abdomen posture, the *E. culicivora* juvenile only rarely alerts its prey by touching a leg. Once in position underneath, the juvenile lunges upward and grabs hold of the mosquito. The attacked mosquito may take flight with the spider on board, only to drop to the ground a few seconds later, presumably having succumbed to the spider's venom. Non-anopheline mosquitoes, with their bodies held about parallel to the substratum, do not afford the small *E. culicivora* juveniles comparable ease of access and, consistent with detours being part of an *Anopheles*-specific prey-capture tactic, juveniles do not take detours when the mosquito they encounter is in the non-anopheline posture.

6. THE PREDATOR'S OWN PREY-CLASSIFICATION SYSTEM

Formal scientific taxonomy when specifying a predator's prey is important in the context of understanding food webs, trophic niches and related topics in community ecology (Futuyma & Moreno 1988; Stouffer et al. 2007; Thompson et al. 2012; Pekár & Toft in press). However, a different perspective is required for understanding predatory specialization, and especially preferences and prey-choice behavior, because scientific taxonomy can be actively misleading when the goal is to understand the adaptations by which the predator becomes especially proficient at preying on particular kinds of prey. For example, we can say that *E. culicivora* and *P. wanlessi* are two predators that specialize on and prefer mosquitoes (Culicidae) as prey, but saying no more than this is misleading. It is misleading because it suggests that our human concept of "mosquito" is meaningful to *P. wanlessi* and *E. culicivora*.

The active stages of a mosquito (larva, pupa and adult) differ strikingly in appearance, and live in distinctively different habitats. The adult mosquito is a terrestrial, flying insect with compound eyes and a proboscis, whereas the juvenile is a wingless, legless aquatic insect with no compound eyes and no proboscis. After learning about the mosquito's life cycle, people readily assign the larvae, pupae and adults to a single category called "mosquito". After learning formal scientific taxonomy, we can understand that there are lots of species that, as a group, irrespective of life stage and sex, constitute a particular insect family, Culicidae. As biologists, we understand that the adult females of most, but not all, of these species sometimes feed on vertebrate blood and that, regardless of prior diet, they are all still mosquitoes. Yet, for an understanding of predatory specialization (Jackson & Cross 2011), we need to understand the predator's own prey-classification system. For understanding predatory specialization by *E. culicivora* and *P. wanlessi*, we need to consider the different ways these two predators experience and classify their prey and it would be far-fetched to suggest that *P. wanlessi* and *E. culicivora* base their specialized, decision-making processes on scientific taxonomy and on an understanding of mosquito life cycles.

We know from prey-choice experiments that *P. wanlessi* and *E. culicivora* classify prey differently (Table 1). Adult and juvenile mosquitoes are different prey categories for *P. wanlessi*, but there is no evidence of juvenile mosquitoes being a relevant prey category for *E. culicivora*. *Anopheles* and non-anopheline mosquitoes are distinctively different prey categories for *E. culicivora*, but this distinction appears to be irrelevant to *P. wanlessi*. For *E. culicivora*, mosquitoes that are carrying blood versus mosquitoes that are not carrying blood is another prey-category distinction that matters, but there is no evidence that this distinction matters to *P. wanlessi*.

No other predators are known to adopt *E. culicivora*'s or *P. wanlessi*'s prey-classification system. We can say this despite experiments having been carried out on another 19 East African salticids (Jackson & Nelson 2012b) in an active effort to determine whether any of these other species resemble *E. culicivora* by targeting blood-carrying mosquitoes as preferred prey. None of these species showed any evidence of discriminating between blood meals (blood-carrying *An. gambiae s.s.* females) and non-blood meals (lake flies or *An. gambiae s.s.* males).

An understanding of the natural diets of salticids would be an interesting complement to understanding predatory specialization on the basis of laboratory experiments. However, field data pertaining to the prey of salticids are scarce and depend on methods considerably different from the methods we have used for determining prey-choice behavior and other behavioral and cognitive features of predatory specialization. Yet, in this instance, it might be useful to speculate about the possibilities.

For example, our guess is that most salticids are ready to eat, and are competent at capturing, mosquitoes when the opportunity arises. After feeding on blood, mosquitoes may become more sluggish and less alert than mosquitoes that have not had recent blood meals and, on this basis, the blood-carrying mosquito may sometimes become more vulnerable to foraging salticids, even when these salticids are not targeting mosquitoes as preferred prey (Roitberg et al. 2003). Perhaps there are salticids that primarily eat mosquitoes without expressing a preference for mosquitoes. Perhaps there are even salticids that eat more mosquitoes than *E. culicivora* or *P. wanlessi* without expressing a preference for mosquitoes. These are all logical possibilities irrespective of whether we can point to specific examples.

Here is another logical possibility and this possibility is especially relevant. If we think about all the predators that might eat mosquitoes (e.g., insectivorous bats and birds), there must be many that have, on the basis of formal scientific taxonomy, considerably wider diet breadth than *E. culicivora* or *P. wanlessi*. Yet, if we consider these other predators' own classification systems, it may usually be the case that "mosquito" is not, for them, a distinct prey category. Often, it may be more accurate to say that, for these predators, a mosquito is just another "bug" (see Lettvin et al. 1959; Ewert 2004; Harland et al. 2012).

7. SPECIALIZED USE OF SEARCH IMAGES

A predator being selectively attentive to a particular type of prey is different from a predator expressing a preference for a particular type of prey, but this distinction has often been blurred in the literature. Selective attention is a thoroughly cognitive topic that entered the ecology literature by another name, "search images". Although there has been interest in search images going back to von Uexküll (1934) (see Bond 2007), it was primarily with Lukas ("Luuk") Tinbergen (1960) that search images as a topic began its peculiar history in ecology. Luuk's brother, Niko Tinbergen, was one of the founders of ethology (Kruuk 2003), but Luuk was an ecologist who did some remarkable field-based research in the Netherlands on insectivorous birds beginning in 1946 but ending abruptly in 1955 with his untimely death at the age of 39 (Baerends & de Ruiter 1960). Luuk Tinbergen's work, published posthumously five years later (Tinbergen 1960), included the search-image hypothesis that made him famous. More specifically, he proposed that, after discovering a particular type of prey, the predators he was studying "got an eye for" or "learned to see" this particular type of prey.

By saying "learning to see", Tinbergen (1960) was apparently proposing that the predator's prior experience with a particular prey type primed it to become selectively attentive to specific features of this particular prey type (Shettleworth 2010). Tinbergen (1960) went further and proposed that predators "perform a highly selective sieving operation on the visual stimuli reaching their retina" (p. 332). By sieving, or filtering, he apparently meant that the predator focussed its attention on specific salient features of the prey, and that it ignored other features. The idea was also that the predator more or less ignored distractors in the environment, where these distractors might be, for example, other kinds of prey that the predator was not being selectively attentive to. There is parallel evidence that sieving is important in the visual-search paradigms adopted by people, where a particular target with a certain configuration of features is attended to within a crowd of distractors (Treisman & Gelade 1980; Treisman 1986; Pashler 1998).

Back in 1960, many biologists were intensively uncomfortable with the notion of non-human animals having cognitive capacities (Wasserman 1997), so it may come as little surprise to learn that search images began as a topic rife with controversy. Discussing animal cognition is now respectable, but the toning down of the search-image controversy began earlier and for the wrong reasons. There was, and continues to be (e.g., Ishii & Shimada 2010), confusion about the critical distinction between search images and preference, with the confusion this causes being compounded by the widespread tendency to ignore the distinction between preference and diet.

Too often, conclusions about animals using search images have been made without the required evidence from well-designed cognitive experiments. In appropriately designed search-image experiments, the test subject should experience prior exposure to a specific priming stimulus, after which there should be trials designed for determining whether the test subject has become selectively attentive to specific stimulus features (Shettleworth 2010). For example, a carefully designed experiment might show that prior exposure to a specific prey type primes a predator to be selectively attentive to visual features of this prey type (Jackson & Li 2004).

Tinbergen (1960) proposed that the birds he studied acquired their search images gradually by a process now known as perceptual learning (Sagi 2011; Watanabe & Sasaki 2015) and, ever since Tinbergen, the idea that the target stimulus is learned has dominated the experimental search-image literature. This has, in turn, biased search-image research toward experiments in which test subjects are repeatedly exposed to a priming stimulus (Royama 1970; Gendron & Staddon 1983; Gendron 1986). The underlying hypothesis is that, by perceptual learning, an individual gradually assembles a template or prototype that is then deployed in the service of detecting and identifying stimuli that match the prototype (Shettleworth 2010). However, the question of whether search images are acquired by perceptual learning is conceptually distinct from the more basic question of whether an animal uses search images at all (i.e., questions about origins are distinct from the question of whether the animal becomes selectively attentive to specific target stimulus features after exposure to a specific priming stimulus).

This conceptual distinction has been important in our own research (Cross & Jackson 2010b) on *E. culicivora*. Our methods were not based on repeatedly exposing *E. culicivora* to priming stimuli and instead we proposed that *E. culicivora* is innately prepared to deploy selective attention to a specific target stimulus even after a single exposure to an appropriate priming stimulus. Being innately prepared means having a capacity for accessing an innate template corresponding to specific stimuli an animal might encounter in its environment. In biology, the best known examples related to "innate templates" may be from research on the ontogeny of bird song (Marler 1952; Konishi 1965; Catchpole & Slater 1995). With bird song, it is proposed that juveniles rely on innate auditory templates that direct attention to a narrow array of natural sounds (also see Gottlieb 1997).

Something else was unconventional about our research on *E. culicivora* (Cross & Jackson 2010b). We considered search images for opposite-sex conspecifics (i.e., potential mates) as well as for prey. However, search images, being fundamentally about selective attention, are not exclusive to predatory strategies. For distinguishing between selective attention and preference, a search-image experiment should include trials in which the stimulus is difficult to identify (cryptic) and other trials in which the stimulus is easy to identify (conspicuous). The rationale for designing experiments in this way is an expectation that deploying selective attention will be especially beneficial when the target stimulus is hard to detect. When the target stimulus is easy to detect, a stronger expression of preferences can be expected.

Before each trial began, we confined the test spider (an adult *E. culicivora* male or female) inside a glass priming chamber for 10 min and, within this chamber, the test spider could see, but not contact, lures made from blood-carrying mosquitoes or lures made from potential mates. We also included no-lure control trials. After the single priming exposure, the test spider could enter a glass arena and, from inside this arena, the test spider had an opportunity to find a mosquito or a mate. It could see, but not contact, the lures behind the glass and it could get close to a lure by walking into a glass tube that protruded out from the arena. When the test spider entered a tube and stayed there, we recorded the outcome of the trial as being an instance of the test spider having found the lure corresponding to the tube it entered.

In cryptic trials, we partially obscured the lures by situating them behind nylon netting. We also situated distractors next to the lures, distractors being other cork discs on which no prey or mates were mounted. In conspicuous trials, the netting and distractors were absent. No test spider was used more than once and, consistent with our interest in innate search images, we also ensured that test spiders had no prior experience with blood-carrying mosquitoes or with potential mates before being used in an experiment.

In congruent trials, the test spider inside the arena could view a target stimulus (mosquito or mate) that was the same as the priming stimulus. In incongruent trials, the target stimulus was not the same as the priming stimulus. As predicted, no significant priming effects were detected when the lures were conspicuous (i.e., when the experimental condition minimized the need for selective attention). However, when the lures were cryptic (i.e., when the experimental condition maximized the need for selective attention), significantly more spiders found the lure after congruent priming than after incongruent priming or after no priming (Cross & Jackson 2010b).

Besides becoming more effective at finding a congruent stimulus after priming, *E. culicivora* also became less effective at finding an incongruent stimulus after priming (Cross & Jackson 2010b). For example, when priming came from seeing a mate, the number of spiders that found a cryptic mosquito was significantly fewer than the number of spiders that found a cryptic mosquito in the no-priming control. Similar trade-off, or interference, effects are known from research on birds and mammals (Pietrewicz & Kamil 1979; Bond 1983; Dukas & Kamil 2000; Kamil & Bond 2006), and it is widely accepted that, even for animals with brains much larger than a spider's, deploying selective attention is cognitively demanding (Desimone 1998; Pashler 1998). We might envisage cognitive resources being tied up when an animal is selectively attentive to objects of one type, and we might propose that a reduction in available cognitive resources impairs an animal's ability to detect and identify other salient objects (Dukas & Kamil 2000). Yet specifying what these cognitive resources are, and how they are used by selective attention, remains unresolved (Cowan 2010; Awh et al. 2007; Mandler 2013).

The findings from our experiments (Cross & Jackson 2010b) illustrate that, for *E. culicivora*, use of selective attention is linked innately to blood-carrying mosquitoes as prey and a drawn-out perceptual-learning process is unnecessary. One exposure apparently prepares *E. culicivora* to become selectively attentive to this particular prey type, and this preparedness is part of what "predatory specialization" means for *E. culicivora*.

8. OLFACTORY SEARCH IMAGES AND CROSS-MODALITY PRIMING

"Image" in "search image" may suggest imagery (Albers et al. 2013), but we are not proposing that salticids are literally looking inward at pictures that they carry around in their heads (Kennedy 1992; Pylyshyn 2003). Search images pertain to selective attention, not pictures (Kamil & Bond 2006; Jackson & Cross 2011). Moreover, as our research on *E. culicivora* illustrates, search images do not have to be based on vision. *Evarcha culicivora* also specializes at using olfactory search images.

The testing protocol used in the olfactory search-image experiments (Cross & Jackson 2010c) had similarities to the protocol used in the visual search-image experiments. Test spiders were first primed by exposure to the odor of blood-carrying mosquitoes or the odor of potential mates before being presented with an opportunity to find the source of either the prey odor or the mate odor. At no point could the test spider see the source of the priming odor or the source of the test odor, and the test odor was either congruent or incongruent with the priming odor.

For test odors, we needed an olfactory analogue of the conspicuous-cryptic distinction in the visual search-image experiments. Our solution was to present a test odor in conjunction with a masking odor. The masking odor came from *Lantana camara* (L.), a plant species that *E. culicivora* visits for nectar meals (Kuja et al. 2012), and it is known that *E. culicivora* detects the odor of this plant species (Cross & Jackson 2009a, Nelson et al. 2012; Nelson & Jackson 2013). "Conspicuous" meant that no masking odor from *L. camara* was present.

In the olfactory search-image experiments (Cross & Jackson 2010c), as in the visual search-image experiments (Cross & Jackson 2010b), the cryptic-conspicuous comparison was critical for distinguishing between selective attention and preference. When the test odor was cryptic, significantly more test spiders found the congruent odor, but there was no significant priming effect when the odor was conspicuous. Moreover, *E. culicivora* became less effective at finding an incongruent odor after priming. For example, when the task was to find prey odor that was cryptic, the number of spiders that found this odor after being primed by smelling mates was significantly fewer than after no priming. These findings suggest that selective olfactory attention, like selective visual attention, is subject to substantial capacity limitations.

Perceptual learning is an unlikely explanation for the findings from the olfactory and the visual search-image experiments because *E. culicivora* had only had one prior exposure to the priming stimulus, with no opportunity to eat, mate or have any other experience that might correspond to the conventional usage of the term "reinforcement" in learning theory (Estes 1962; Shanks 2010). Yet we have to concede that, although one-trial perceptual learning seems unlikely, it cannot be entirely dismissed on the basis of these search-image experiments.

However, findings from cross-modality priming experiments completely rule out the remote possibility of even one-trial perceptual learning. In these experiments (Cross & Jackson 2009b), smelling blood-carrying mosquitoes primed selective attention to visual stimuli from specifically blood-carrying mosquitoes and seeing blood-carrying mosquitoes primed selective attention to olfactory stimuli from specifically blood-carrying mosquitoes. The spiders in these experiments had never seen or smelled mosquitoes before being tested. Only one exposure to the priming stimulus sufficed, and this priming stimulus was in a modality different from the target stimulus. The findings from these experiments imply that, for *E. culicivora*, smelling blood-carrying female mosquitoes calls up an innate visual search image for blood-carrying female mosquitoes and seeing blood-carrying female mosquitoes calls up an innate olfactory search image for blood-carrying female mosquitoes.

9. WORKING MEMORY AND INNATE RELEASING MECHANISMS

Innate search images can be defined more precisely. Instead of literally being pictures in an animal's head, search images are specific feature-detection mechanisms. Investigating innate search images in our experiments was unconventional but important in the context of understanding predatory specialization because we show that, for *E. culicivora*, part of what predatory specialization means is having innate feature-detection mechanisms that can function in the context of being selectively attentive to blood-carrying mosquitoes.

For putting the idea of innate feature-detection mechanisms into context, we can revisit the founding days of ethology and the legacy of Luuk Tinbergen's brother, Niko. Innate feature detectors were called the innate releasing mechanisms (IRMs) in Lorenz's once famous, but now largely forgotten, psycho-hydraulic model of instinctive behavior (Tinbergen 1951; Lorenz 1965). In Lorenz's model, a specific stimulus (the releaser) was likened to a key that, by fitting into a lock (the IRM), releases the expression of a fixed action pattern. These are metaphorical, not literal, locks and keys. "Image" in a "search image" is another metaphor. However, when trying to understand search images, the lock-and-key metaphor may be less misleading than the metaphor of animals looking at pictures in their heads.

For *E. culicivora*, part of what we mean by specialization is using innate feature-detector mechanisms when deploying selective attention (Cross & Jackson 2009b, 2010b, 2010c). An experimental design based on the cryptic-conspicuous distinction was critical for confirming that the findings revealed selective attention instead of preference. Controlling for variation in prior experience was critical for confirming that the feature-detection mechanisms used in conjunction with selective attention were innate.

Consistent with the widely held view that deploying selective attention is a capacity-limited, cognitive task, *E. culicivora*'s performance was impaired in the incongruent trials. For understanding why these limitations occur, we need to consider working memory. Although long-term memory and short-term memory are often referred to as though they are passive archives, working memory is envisaged as having an active, critical role in cognition (Baddeley 1986, 2012). More specifically, it has been proposed that working memory includes mechanisms by which priority information is made immediately accessible to other cognitive processes. Selective attention is one of these other processes. In *E. culicivora*'s case, we propose that, after exposure to priming stimuli, an innate mosquito-specific feature-detection mechanism is loaded into working memory and that this specific feature-detection mechanism is coupled with selective attention in working memory. Saying it is "priority information" means that this feature-detection mechanism is in an activated state, ready for immediate use. Capacity limits are envisaged as a consequence of there being severe competition for this priority status in working memory (Rouder et al. 2008).

10. A PREDATOR THAT LIKES US AND EATS OUR ENEMIES

Targeting *Anopheles* as preferred mosquitoes is one of *E. culicivora*'s more intriguing characteristics because *Anopheles* is the mosquito genus to which all human-malaria vectors belong (Spielman & D'Antonio 2001). Malaria, one of the most significant diseases in human history (Cox 2010), continues to be an especially serious public-health issue in sub-Saharan Africa where more than 90% of deaths from malaria occur each year (Murray et al. 2012).

Some of the questions people ask about mosquito terminators can be disconcerting. Many people want to know whether we plan to release millions of these spiders into the wild, especially throughout Africa and Asia, without considering any of the potential consequences on local ecosystems. We have also been asked surprisingly often whether *E. culicivora* is a malaria vector. The idea seems to be that the spider gets malaria by taking human blood from *Anopheles*, with the next step being that, by coming into our homes and biting us, the spider passes malaria on to people. As *E. culicivora* is not the kind of animal that goes around biting people, this question is irrelevant. However, it is also out of step with how malaria works.

Malaria is a disease caused by *Plasmodium* and some related genera (Perez-Tris et al. 2005) of one-cell parasites from the phylum Apicomplexa (Garnham 1966). Many terrestrial vertebrates serve as intermediate hosts in which these parasites reproduce only asexually. People are, on a regular basis, intermediate hosts for *P. vivax*, *P. ovale*, *P. malariae*, *P. knowlesi* and *P. falciparum*. *Plasmodium falciparum*, the most lethal, is the dominant human malaria parasite in sub-Saharan Africa (Guerra et al. 2008).

The term "vectors" is used for the parasite's definitive hosts in which the parasite reproduces sexually. For the *Plasmodium* species that infect people, the definitive hosts are always mosquitoes. When we consider *Plasmodium*'s complicated life cycle based on being adapted to parasitizing specific primary and intermediate hosts (Packard 2007; Cox 2010), it is hard to see any realistic way for a spider to function as a malaria vector. When feeding on human blood, mosquitoes get infected while ingesting the gametocyte stage of *Plasmodium*. In the mosquito's digestive tract, the gametocytes turn into sperm and eggs, zygotes form, the zygotes grow into ookinetes, the ookinetes turn into bags of sporozoites and then, after bursting out of the ookinete, the sporozoites get packed into a mosquito's salivary glands. We get infected with the sporozoites when an infected mosquito punctures our skin and injects sporozoites along with the anti-clotting agents in its saliva (Garnham 1966).

It is exceedingly difficult to make a rational case for worrying about malarial spider bites. Being bitten by *E. culicivora* would be a freak event. We have no knowledge of anybody ever being bitten by *E. culicivora* and we have never seen anything even remotely like an attempt to bite anybody. Even if some rogue *E. culicivora* one day bites somebody, injecting saliva from sporozoite-packed salivary glands is utterly far fetched. Mosquitoes, not spiders, are malaria vectors.

More than 3,500 mosquito species have been described, with close to 500 of these species belonging to the genus *Anopheles*. About 70 *Anopheles* species are known to be competent human-malaria vectors (Harbach 2004; Godfray 2013). *Anopheles gambiae* gets the most attention (Spielman & D'Antonio 2001), but discussing *An. gambiae* quickly becomes complicated because, instead of being a single species, this is a species complex (Coetzee et al. 2000) with the constituent species being behaviorally different, but morphologically indistinguishable, and molecular methods are necessary for distinguishing between these species (Fanello et al. 2002). One of these species, *An. gambiae sensu stricto*, has special characteristics that make it the most notorious of *P. falciparum*'s vectors (Sinka et al. 2010), and one of these characteristics is anthropophily. For *An. gambiae s.s.*, anthropophily means taking blood meals primarily from people (White 1974) and being especially proficient at detecting human odor (Takken & Knols 1999; Carey et al. 2010).

There is no evidence from vision-based or olfaction-based prey-choice experiments to suggest that *E. culicivora* distinguishes between different *Anopheles* species (Jackson & Cross unpubl.). However, like *An. gambiae s.s.* (Spielman & D'Antonio 2001), *E. culicivora* is found especially often in or near buildings occupied by people (Wesolowska & Jackson 2003). Frequenting the same habitats might result in *E. culicivora* preying especially often on *An. gambiae*. This became the rationale for investigating whether, like *An. gambiae s.s.*, *E. culicivora* might be anthropophilic.

Human foot odor is especially attractive to *An. gambiae s.s.* and dirty socks make a convenient foot-odor source to use in experiments, as long as you get the right person to donate the socks because people vary considerably in how strongly they attract *An. gambiae s.s.* (Mukabana et al. 2002; Omolo et al. 2013). For our olfactometer experiments (Cross & Jackson 2011), we used socks that had been worn by the same anonymous donor whose socks had been the most attractive to *An. gambiae s.s.* in an earlier study (Njiru et al. 2006). Our findings showed that the time *E. culicivora* spent near air blown over this donor's socks was significantly longer than the time it spent near air blown over clean socks.

By responding to human odor, *An. gambiae s.s.* can find and bite people for direct blood meals. By responding to human odor, *E. culicivora* does not find people to bite, but anthropophily might be a way for *E. culicivora* to find the anthropophilic mosquitoes that are heavy with blood after biting people.

11. BLOOD AS PERFUME

For answering questions about a predator's prey-choice behavior in the context of optimal foraging, it is conventional to consider energy rewards and the acquisition of important nutrients (Pyke 1984). However, for *E. culicivora*, the conventional focus on energy and nutrients leaves out something important. For this spider, there is an unusual link between prey-choice and mate-choice decisions. By eating blood-carrying mosquitoes, both sexes of *E. culicivora* acquire an odor (a "perfume") and olfactometer experiments show that this perfume renders both sexes more attractive to potential mates (Cross et al. 2009). The implication is that *E. culicivora* specializes at killing blood-carrying mosquitoes for sex as well as for food.

It might be tempting to suggest, as a straightforward sensory-exploitation explanation (Arnqvist 2006), that *E. culicivora* smells like what it eats, and a hypothesis is that being attracted to the odor of blood-carrying mosquitoes is no different from *E. culicivora* being attracted to the odor of a conspecific individual that has been feeding on blood-carrying mosquitoes. However, other findings imply that this explanation is too simplistic. Although the odor of potential mates that had been on a blood diet was more attractive to test spiders than the odor of potential mates that had been on a non-blood diet, there was no evidence to suggest that same-sex conspecific individuals (Cross et al. 2009) or opposite-sex heterospecific individuals (Cross & Jackson 2013) also became attractive after being maintained on the same blood diet.

Even a single blood meal suffices to make *E. culicivora* more attractive to potential mates, but this perfume dissipates (Cross et al. 2009). Even just a day later, *E. culicivora* becomes significantly less attractive. These findings have an interesting implication. For *E. culicivora*, killing mosquitoes may be motivated by more than hunger and, even when nutritionally satiated, *E. culicivora* is a predator that goes on killing mosquitoes for perfume.

12. ADAPTIVE TRADE-OFFS

Something disconcerting often happens when we discuss the ways in which *E. culicivora* and *P. wanlessi* specialize at preying on mosquitoes. Some people automatically assume we must be saying that these two predators are limited to preying on mosquitoes alone. There appears to be a widespread habit of blurring the distinction between specialization (the adaptations that make a predator especially proficient at targeting particular types of prey) and hypotheses about limitations being a consequence of becoming specialized (e.g., Vamosi et al. 2014). Blurring this distinction often seems to come out of acknowledging that, at some level, ideas about trade-offs are fundamental in biology (Hutchinson 1959; Levins 1968; Stearns 1989; Garland 2014), but we need something more.

On a case-by-case basis, we need to determine the threshold at which trade-offs actually become important (Roff & Fairbairn 2007) and we need to determine precisely how these trade-off effects are expressed.

Saying that "the jack of all trades is the master of none" adds nothing useful. This is a figure of speech, not a scientific principle, and the underlying intuition is debatable when applied to people as well as when applied to non-human predators. In fact, there is no shortage of findings that are contrary to the jack-of-all-trades intuition (e.g., Whitlock 1996), with many of the examples that challenge this intuition having come from salticids (Jackson & Hallas 1986; Harland et al. 2012; Jackson & Cross 2013).

On the whole, functionally incompatible morphology might be the context most likely to give us convincing examples of adaptive trade-offs (Garland 2014). For example, specialized cheliceral morphology might make a spider especially proficient at capturing and feeding on particular types of prey and, at the same time, render it less proficient at capturing and feeding on other types of prey (Řezáč et al. 2008). This is because a spider comes equipped with a single pair of chelicerae and cheliceral morphology changes only slowly during the spider's lifetime. However, we should pause before making the major leap of assuming that behavior is automatically subject to functional incompatibility at a level similar to which functional incompatibility often seems to apply to morphology.

Although there may be situations in which a predator cannot deploy two or more distinctively different prey-capture methods at the same time, it is obvious that switching from one behavior routine to another often happens in a hurry. All the same, it might still be argued that neural circuits underpin behavioral routines and that these circuits are basically morphological and, as such, can be envisaged as being fixed in place in much the same way that cheliceral morphology is fixed in place. However, this argument is based on an unsubstantiated assumption (Eberhard 2011; Eberhard & Wcislo 2011) that the brain of a spider is too small to accommodate the volume and variety of neural structure needed for deploying repertoires of many distinctly different predatory routines, each routine being well-adapted for making the predator proficient when targeting distinctly different prey types. Emphatic rebuttals of this assumption are easily found in the predatory strategy of *Portia*. There are many examples of single individuals of *Portia* making rapid opportunistic switches between distinctively different innate prey-capture routines (Harland & Jackson 2004). Switching between prey-capture routines is also characteristic of mosquito terminators, again without severe trade-offs being evident.

The blurring of the distinction between specialization and limitations as potential consequences of specialization often seems to be based on accepting trade-off hypotheses as foregone conclusions. However, if trade-off effects are severe enough to justify accepting them as foregone conclusions, then why are they not more readily apparent? For example, *P. wanlessi* specializes in different ways at preying on adult and on juvenile mosquitoes. *Evarcha culicivora* specializes at preying on adult mosquitoes, but is not known to target juvenile mosquitoes. Yet there is no evidence to suggest trade-offs whereby *P. wanlessi* has become less proficient than *E. culicivora* at preying on adult mosquitoes. Of course, absence of evidence is not evidence of absence. There can always be questions concerning whether we have attempted to find trade-off effects with sufficient determination or in the right way. Nor are we proposing that trade-off effects are completely irrelevant for understanding the predatory strategies of *Portia* and the mosquito terminators, but we do propose that precisely how any specific trade-offs are expressed, and precisely how severe any particular trade-offs might be, needs to be determined on the basis of solid evidence and well formulated hypotheses. We also emphasize that answering these questions about potential consequences of specialization must be kept conceptually separated from our evidence-based conclusion that *P. wanlessi* and *E. culicivora* are highly specialized predators.

13. OBLIGATE PREDATION ON SPECIFIC TYPES OF PREY

Asking whether a predator is specialized at preying on a particular type of prey is conceptually distinct from asking whether a predator is an obligate predator of a particular type of prey. Obligate means that the predator must eat the prey in question, but evidence that a predator is an obligate predator of a specific prey type is not automatically evidence that the predator is restricted to eating only this prey. As spiders are known sometimes to acquire balanced diets by getting different essential nutrients from different types of prey (Greenstone 1979: Mayntz et al. 2005), becoming an obligate predator of more than one prey type is a possibility that should be considered (i.e., being an obligate predator of one prey type does not rule out the possibility of also being an obligate predator of one or more other prey types).

We have been interested in a hypothesis that *E. culicivora* is metabolically specialized on the blood meals it acquires from mosquitoes, with the rationale for this hypothesis coming from our efforts to maintain cultures of this predator in the New Zealand laboratory where we have no reliable access to blood-carrying mosquitoes for rearing. Usually we have thriving *E. culicivora* cultures for one generation and then they die off in the second and third generation. This problem has not been solved by mixing expired blood from a local blood bank with the food given to *Drosophila melanogaster* Meigen and then letting *E. culicivora* feed on the *Drosophila* (Dolev & Nelson 2014). In the Kenya laboratory, it is much the same. *Evarcha culicivora* cultures maintained on lake flies or male mosquitoes (i.e., non-blood diets) are good for one generation, only to die off in the 2nd and 3rd. Yet, when supplied with blood-carrying mosquitoes as prey, *E. culicivora* cultures in Kenya have been sustained for more than a decade.

If corroborated, the hypothesis that *E. culicivora* is an obligate predator of blood-carrying mosquitoes will be of interest because there is no hint of an obligation to eat this particular prey until the second generation. Moreover, being an obligate predator does not imply that *E. culicivora* is restricted to feeding solely on blood-carrying mosquitoes. In fact, preliminary findings suggest that the optimal diet for *E. culicivora* is blood-carrying mosquitoes plus lake flies (i.e., the performance of cultures maintained on a mixed diet is better than the performance of cultures maintained on blood-carrying mosquitoes alone).

It may be tempting to say that an obligate predator of a particular prey type is more highly specialized than a predator that adopts highly specialized prey-specific prey-capture behavior when targeting a particular prey type but without being an obligate predator of this particular prey type. However, again, *Portia* is instructive. In Australia's Queensland rainforests, *P. fimbriata* Doleschal adopts a strikingly specialized method for preying on *Euryattus* Thorell sp. indet., another salticid species from the same habitat. *Euryattus* is an unusual salticid (Jackson 1985) because the adult female's nest is a rolled-up dead leaf suspended by silk guylines from a tree trunk, a rock ledge or the vegetation. When quiescent, *Euryattus* females remain within the enclosed space defined by the rolled-up leaves. *Euryattus* males locate the guylines, move slowly onto the leaf and then make distinctive courtship signals by suddenly and strongly flexing their legs to make the leaf rock back and forth. The female responds by coming out of the nest and then she either mates with the male or else she drives him away. When *P. fimbriata* sees one of these leaf nests, something similar happens. *Portia fimbriata* goes slowly down a guyline and onto the leaf. Once on the leaf, *P. fimbriata* settles next to one of the openings in the rolled-up leaf and then makes intermittent signals. These signals mimic the courtship signals of *Euryattus* males and, instead of being greeted by a conspecific male, the female coming out of her nest in response to the signals is ambushed by *Portia* (Jackson & Wilcox 1990).

Although this is an example of *P. fimbriata* adopting highly specialized *Euryattus*-specific predatory behavior, and although "specialize" is definitely the correct word to use, the very same *P. fimbriata* individuals also adopt other highly specialized prey-capture behavior when encountering other types of prey and there is no evidence that *P. fimbriata* is an obligate predator of *Euryattus* females. For example, cultures of *P. fimbriata* have been maintained for close to a decade without any individual of *P. fimbriata* in these cultures ever having fed on *Euryattus*. Whether or not *P. fimbriata* is an obligate predator of *Euryattus* emphatically has no bearing on the conclusion that *P. fimbriata* is highly specialized at preying on *Euryattus*.

Unpublished observations on *P. wanlessi* are similar. Cultures of *P. wanlessi* were normally maintained on a mixed diet that included adult and juvenile mosquitoes (Jackson et al. 2014), but providing *P. wanlessi* with juvenile mosquitoes in water was a laborious procedure. There were times when we kept excess individuals of *P. wanlessi* for two generations without any aquatic prey and yet there were no noticeable ill effects on *P. wanlessi*. Although these findings are not from a carefully designed experiment, they at least strongly suggest that *P. wanlessi* is not an obligate predator of juvenile mosquitoes. Yet none of this has any bearing on the evidence-based conclusion that *P. wanlessi* is highly specialized at preying on juvenile mosquitoes. The biology of *Portia* and of mosquito terminators illustrates emphatically that "specialized" and "obligate" refer to different things.

14. MOSQUITO TERMINATORS LEADING US THROUGH A CONCEPTUAL JUNGLE

Literature on predatory specialization is easy to find, but not always easy to read, and it becomes a conceptual jungle when natural diet, adaptive trade-offs, obligate predation and related topics blur into the meaning of specialization. Yet we appreciate how the ways people first become interested in predatory specialization can encourage different ways of thinking about this topic. A theory-based path may be common, but the mosquito-terminator research had a more casual origin. It began when something unusual was noticed in western Kenya, where we live. Many salticids share houses with people and with insects. Sometimes lake flies cover the walls inside houses and look like six-legged grasses in a hexapod prairie, complete with herds of grazing salticids. Slowly it became apparent that one salticid species in particular was eating primarily mosquitoes and, in the process, was taking blood, probably our blood, from the mosquitoes. We called this salticid the mosquito terminator, but it later got a scientific name, *Evarcha culicivora* (Wesolowska & Jackson 2003). Step by step, with hypotheses leading to experiments and then ever more hypotheses and more experiments, a research program developed. Thinking about conceptual distinctions and an emphasis on detail was characteristic of this research from the very beginning.

It is easy to imagine how mosquito-terminator research might have developed along a different path. Many people apparently assume, incorrectly, that we began with a goal of finding a potential biological control agent for malaria vectors. If that had been the way we began, then the literature on pest control would probably have been a stronger initial influence on our thinking.

In the pest-control literature, there is a tradition of thinking about predators as being either specialists or generalists, and then comparing the effectiveness of "specialists" with the effectiveness of "generalists" in controlling particular pest species (Riechert & Lockley 1984; Gurr & Wratten 2000). Instead of determining whether a predator is a specialist in the context of whether it is especially proficient at, and adaptively fine tuned to, targeting a particular pest species, a different topic often seems to nudge its way in unannounced and without explanation. The "other topic" in the context of biological control is especially often a discussion of whether an animal is an obligate predator of a pest species, with the actual topic being discussed becoming all the more confusing when a discussion of "obligate" blurs into a discussion about predators that are restricted to eating solely the specified pest species.

Here is an interesting example of how this kind of conceptual blurring can be misleading. When comparing the efficacy of specialist and generalist predators in the biological control of pests, the strategy of the specialist has been called "search and destroy" and the strategy of the generalist has been called "lying in wait" (Symondson et al. 2002). We like these colorful descriptions, but using them for stipulating how specialists differ from generalists is misleading. "Search and destroy" is a highly appropriate description for the strategy of *E. culicivora*, a predator that singles out blood-carrying mosquitoes as preferred prey and, like Arnold Schwarzenegger in the James Cameron movie The Terminator (1984), appears to push aside whoever gets in the way (e.g., lake flies) while going after the targeted victim (i.e., the mosquito). Even better, *E. culicivora* singles out malaria vectors (*Anopheles*) as preferred mosquitoes, seeks them out and destroys, or terminates, them. Yet, for *E. culicivora*, a mosquito specialist, "lying in wait" is also an appropriate description.

We suspect that, in the biological control literature, when a specialist's strategy is said to be "search and destroy" and a generalist's strategy is said to be "lying in wait," the intended comparison is actually between an obligate and restricted predator of a pest species and another predator that is not an obligate or restricted predator of the same pest species. When saying "lying in wait," the idea seems to be that a predator that eats the same pest species, without being an obligate and restricted predator of this pest species, can hang on in the environment by eating something else when the pest species is rare or absent and then eat the pest species when it becomes more abundant.

However, *E. culicivora* makes a mess of this conceptual scheme because it is a mosquito specialist that practices search-and-destroy predation when blood-carrying mosquitoes are present and also has the capacity to practice lying-in-wait predation if its preferred prey is not around. It is *E. culicivora*'s predatory and prey-choice behavior, not its being an obligate predator, that makes "search and destroy" an appropriate description. "Lying in wait" is also an appropriate description for *E. culicivora*, independent of "search and destroy" being appropriate.

Paracyrba wanlessi is also appropriately described as a lie-in-wait and as a search-and-destroy predator, and *P. wanlessi*'s predatory strategy and preference profile emphasize that a single individual can be a "search-and-destroy" predator in one way with one prey type (e.g., adult mosquitoes away from water) and in another way with another prey type (e.g., juvenile mosquitoes in water).

Whether mosquito terminators can be exploited by people in the context of mosquito control is a different question. Bamboo as a habitat may make *P. wanlessi* a less obvious candidate for a role in pest control, but *E. culicivora* willingly goes into our houses and kills malaria vectors. Encouraging people to welcome these guests into their homes sounds like a good idea. Yet it is hard to be optimistic about educating the lay public when there are even entomologists, people who work with maggots and cockroaches, who find spiders repulsive (Vetter 2013).

ACKNOWLEDGMENTS

We thank Stephene Abok Aluoch, David Tom Omondi, Kevin Ochieng, Maurice Ayawo, Godfrey Otieno Sune and Silas Orima for their assistance with laboratory and field work in Kenya. Our research was supported by grants from the Royal Society of New Zealand (Marsden Fund (UOC305, UOC1301) and James Cook Fellowship (02/05)), the National Geographic Society ((8676-09, 6705-00)), the Foundation of Research, Science and Technology (UOCX0903) and the US National Institutes of Health (R01-AI077722). We would especially like to thank the icipe community, including three successive Director Generals (Hans Herren, Christian Borgeimester and Segenet Kelemu), for the continuing interest and support given to the mosquito-terminator work.

LITERATURE CITED

Albers, A.M., P. Kok, I. Toni, H.C. Dijkerman & F.P. de Lange. 2013. Shared representations for working memory and mental imagery in early visual cortex. Current Biology 23:1427–1431.

Arnqvist, G. 2006. Sensory exploitation and sexual conflict. Philosophical Transactions of the Royal Society of London Series B 361:375–386.

Awh, E., B. Barton & E.K. Vogel. 2007. Visual working memory represents a fixed number of items regardless of complexity. Psychological Science 18:622–628.

Baddeley, A. 1986. Working Memory. Oxford University Press, Oxford.

Baddeley, A. 2012. Working memory: theories, models, and controversies. Annual Review of Psychology 63:1–29.

Baerends, G.P. & L. de Ruiter. 1960. Foreword. Archives Neerlandaises de Zoologie 13:258–263.

Beadle, L.C. 1981. The inland waters of tropical Africa: an introduction to tropical limnology. Longman, London.

Becker, N., D. Petric, M. Zgomba, C. Boase, M. Madon & C. Dahl, et al. (2010). Mosquitoes and Their Control. Springer, Berlin.

Berenbaum, M.R. 1996. Introduction to the symposium: on the evolution of specialization. American Naturalist 148(Supplement):S78−S83.

Bishop, S.C. & R.C. Hart. 1931. Notes on some natural enemies of the mosquito in Colorado. Journal of the New York Entomological Society 39:151–157.

Bond, A.B. 1983. Visual search and selection of natural stimuli in the pigeon: the attention threshold hypothesis. Journal of Experimental Psychology: Animal Behavior Processes 9:292–306.

Bond, A.B. 2007. The evolution of color polymorphism: crypticity, searching images, and apostatic selection. Annual Review of Ecology, Evolution and Systematics 38:489–514.

Breene, R.G., M.H. Sweet & J.K. Olson. 1988. Spider predators of mosquito larvae. Journal of Arachnology 16:275–277.

Carey, A.F., G. Wang, C.-Y. Su, L.J. Zwiebel & J.R. Carlson. 2010. Odorant reception in the malaria mosquito *Anopheles gambiae*. Nature 464:66–71.

Carpenter, G.D.H. 1920. A Naturalist on Lake Victoria. Unwin, London.

Catchpole, C.K. & P.J.B. Slater. 1995. Bird song: biological themes and variations. Cambridge University Press, Cambridge.

Cerveira, A.M. & R.R. Jackson. 2011. Interpopulation variation in kairomone use by *Cyrba algerina*, an araneophagic jumping spider from Portugal. Journal of Ethology 29:121–129.

Chhilar, J.S. & S. Chaudhry. 2010. First report of a biting midge *Culicoides anophelis* parasitizing mosquito *Anopheles stephensi* from north-western India. Journal of Experimental Sciences 1:3–6.

Chu, F.I. 1959. Four species of the genus *Culicoides* (Diptera: Heleidae) from Hainan island, south China. Acta Entomologica Sinica 9:161–165.

Clements, A.N. 1992. Biology of Mosquitoes: Development, Nutrition, and Reproduction. CABI Publishing, Oxon.

Clements, A.N. 1999. The Biology of Mosquitoes: Sensory Reception and Behaviour. CABI Publishing, Oxon.

Coetzee, M., M. Craig & D. le Sueur. 2000. Distribution of African malaria mosquitoes belonging to the *Anopheles gambiae* complex. Parasitology Today 16:74–77.

Cowan, N. 2010. The magical mystery four: how is working memory capacity limited, and why? Current Directions in Psychological Science 19:51–57.

Cox, F.E.G. 2010. History of the discovery of the malaria parasites and their vectors. Parasites & Vectors 3:5.

Cross, F.R. & R.R. Jackson. 2009a. Odour-mediated response to plants by *Evarcha culicivora*, a blood-feeding jumping spider from East Africa. New Zealand Journal of Zoology 36:75–80.

Cross, F.R. & R.R. Jackson. 2009b. Cross-modality priming of visual and olfactory selective attention by a spider that feeds indirectly on vertebrate blood. The Journal of Experimental Biology 212:1869–1875.

Cross, F.R. & R.R. Jackson. 2010a. Mosquito-specialist spiders. Current Biology 20:R622−R624.

Cross, F.R. & R.R. Jackson. 2010b. The attentive spider: search-image use by a mosquito-eating predator. Ethology 116:240–247.

Cross, F.R. & R.R. Jackson. 2010c. Olfactory search-image use by a mosquito-eating predator. Proceedings of the Royal Society of London Series B 277:3173–3178.

Cross, F.R. & R.R. Jackson. 2011. Olfaction-based anthropophily in a mosquito-specialist predator. Biology Letters 7:510–512.

Cross, F.R. & R.R. Jackson. 2013. The functioning of species-specific olfactory pheromones in the biology of a mosquito-eating jumping spider from East Africa. Journal of Insect Behavior 26:131–148.

Cross, F.R., R.R. Jackson & S.D. Pollard. 2009. How blood-derived odor influences mate-choice decisions by a mosquito-eating predator. Proceedings of the National Academy of Sciences (USA) 106:19416–19419.

Curio, E. 1976. The Ethology of Predation. Springer-Verlag, Berlin.

Cushing, P.E. 2012. Spider-ant associations: An updated review of myrmecomorphy, myrmecophily, and myrmecophagy in spiders. Psyche 2012:151989.

Desimone, R. 1998. Visual attention mediated by biased competition in extrastriate visual cortex. Philosophical Transactions of the Royal Society of London Series B 353:1245–1255.

Dolev, Y. & X.J. Nelson. 2014. Innate pattern recognition and categorization in a jumping spider. PLoS ONE 9:e97819.

Dukas, R. & A.C. Kamil. 2000. The cost of limited attention in blue jays. Behavioral Ecology 11:502–506.

Eberhard, W.G. 2011. Are smaller animals behaviourally limited? Lack of clear constraints in miniature spiders. Animal Behaviour 81:813–823.

Eberhard, W.G. & W.T. Wcislo. 2011. Grade changes in brain-body allometry: morphological and behavioural correlates of brain size in miniature spiders, insects and other invertebrates. Advances in Insect Physiology 40:155–214.

Edwards, F.W. 1922. On some Malayan and other species of *Culicoides*, with a note on the genus *Lasiohelea*. Bulletin of Entomological Research 13:161–167.

Estes, W.K. 1962. Learning theory. Annual Review of Psychology 13:107–144.

Ewert, J.-P. 2004. Motion perception shapes the visual world of amphibians. Pp. 117–160. *In* Complex Worlds from Simpler Nervous Systems. (F.R. Prete, ed.). MIT Press, Cambridge.

Fanello, C., F. Santolamazza & A. della Torre. 2002. Simultaneous identification of species and molecular forms of the *Anopheles gambiae* complex by PCR-RFLP. Medical and Veterinary Entomology 16:461–464.

Foelix, R.F. 2011. Biology of Spiders, 3rd ed. Oxford University Press, Oxford.

Forster, L.M. 1982. Vision and prey-catching strategies in jumping spiders. American Scientist 70:165–175.

Futami, K., G. Sonye, P. Akweywa, S. Kaneko & N. Minakawa. 2008. Diving behavior in *Anopheles gambiae* (Diptera: Culicidae): avoidance of a predacious wolf spider (Araneae: Lycosidae) in relation to life stage and water depth. Journal of Medical Entomology 45:1050–1056.

Futuyma, D.J. & G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology and Systematics 19:207–233.

Garcia, R. & E.I. Schlinger. 1972. Studies of spider predation on *Aedes dorsalis* (Meigen) in a salt marsh. Proceedings and Papers of the Annual Conference of the California Mosquito Control Association, Inc 40:117–118.

Gardner, B.T. 1964. Hunger and sequential responses in the hunting behavior of salticid spiders. Journal of Comparative and Physiological Psychology 58:167–173.

Garland, T. 2014. Trade-offs. Current Biology 24:R60−R61.

Garnham, P.C.C. 1966. Malaria Parasites and Other Haemosporidia. Blackwell Scientific, Oxford.

Gendron, R.P. 1986. Searching for cryptic prey: Evidence for optimal search rates and the formation of search images in quail. Animal Behaviour 34:898–912.

Gendron, R.P. & J.E.R. Staddon. 1983. Searching for cryptic prey: the effect of search rate. American Naturalist 121:172–186.

Godfray, H.C.J. 2013. Mosquito ecology and control of malaria. Journal of Animal Ecology 82:15–25.

Gottlieb, G. 1997. Synthesizing Nature-Nurture: Prenatal Roots of Instinctive Behavior. Lawrence Erlbaum Associates, Mahwah, New Jersey.

Greenstone, M.H. 1979. Spider feeding behavior optimises dietary essential amino acid composition. Nature 282:501–503.

Greenstone, M.H. 1983. Site-specificity and site tenacity in a wolf spider: a serological dietary analysis. Oecologia 56:79–83.

Guerra, C.A., P.W. Gikandi, A.J. Tatem, A.M. Noor, D.L. Smith & S.I. Hay, et al. (2008). The limits and intensity of *Plasmodium falciparum* transmission: implications for malaria control and elimination worldwide. PLoS Medicine 5:e38.

Gurr, G. & S.D. Wratten. 2000. Biological Control: Measures of Success. Kluwer Academic Publishers, Boston.

Harbach, R.E. 2004. The classification of genus *Anopheles* (Diptera: Culicidae): a working hypothesis of phylogenetic relatiohships. Bulletin of Entomological Research 94:537–553.

Harland, D.P. & R.R. Jackson. 2002. Influence of cues from the anterior medial eyes of virtual prey on *Portia fimbriata*, an araneophagic jumping spider. Journal of Experimental Biology 205:1861–1868.

Harland, D.P. & R.R. Jackson. 2004. *Portia* perceptions: the *Umwelt* of an araneophagic jumping spider. Pp. 5–40. *In* Complex Worlds from Simpler Nervous Systems. (F.R. Prete, ed.). MIT Press, Cambridge, Massachusetts.

Harland, D.P., D. Li & R.R. Jackson. 2012. How jumping spiders see the world. Pp. 133–164. *In* How Animals See the World: Comparative Behavior, Biology, and Evolution of Vision. (O. Lazareva, T. Shimizu & E.A. Wasserman, eds.). Oxford University Press, New York.

Huseynov, E.F., R.R. Jackson & F.R. Cross 2008. The meaning of predatory specialization as illustrated by *Aelurillus m-nigrum*, an ant-eating jumping spider (Araneae: Salticidae) from Azerbaijan. Behavioural Processes 77:389–399.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist 93:145–159.

Ishii, Y. & M. Shimada. 2010. The effect of learning and search images on predator-prey interactions. Population Ecology 52:27–35.

Jackson, R.R. 1985. The biology of *Euryattus* sp. indet., a web-building jumping spider (Araneae, Salticidae) from Queensland: Utilization of silk, predatory behaviour, and intraspecific interactions. Journal of Zoology Series B 1:145–173.

Jackson, R.R. 1992. Eight-legged tricksters: spiders that specialize at catching other spiders. BioScience 42:590–598.

Jackson, R.R. & F.R. Cross. 2011. Spider cognition. Advances in Insect Physiology 41:115–174.

Jackson, R.R. & F.R. Cross. 2013. A cognitive perspective on aggressive mimicry. Journal of Zoology 290:161–171.

Jackson, R.R. & S.E.A. Hallas. 1986. Capture efficiencies of web-building jumping spiders (Araneae, Salticidae): is the jack-of-all-trades the master of none? Journal of Zoology 209:1–7.

Jackson, R.R. & D. Li. 2004. One-encounter search-image formation by araneophagic spiders. Animal Cognition 7:247–254.

Jackson, R.R. & X.J. Nelson. 2012a. Specialized exploitation of ants (Hymenoptera: Formicidae) by spiders (Araneae). Myrmecological News 17:33–49.

Jackson, R.R. & X.J. Nelson. 2012b. *Evarcha culicivora* chooses blood-fed *Anopheles* mosquitoes but other East African jumping spiders do not. Medical and Veterinary Entomology 26:233–235.

Jackson, R.R. & S.D. Pollard. 1996. Predatory behavior of jumping spiders. Annual Review of Entomology 41:287–308.

Jackson, R.R. & M.S. Tarsitano. 1993. Responses of jumping spiders to motionless prey. Bulletin of the British Arachnological Society 9:105–109.

Jackson, R.R. & R.S. Wilcox. 1990. Aggressive mimicry, prey-specific predatory behaviour and predator recognition in the predator-prey interactions of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. Behavioral Ecology and Sociobiology 26:111–119.

Jackson, R.R., R.J. Clark & D.P. Harland. 2002. Behavioural and cognitive influences of kairomones on an araneophagic jumping spider. Behaviour 139:749–775.

Jackson, R.R., D. Li, J.R.W. Woon, R. Hashim & F.R. Cross. 2014. Intricate predatory decisions by a mosquito-specialist spider from Malaysia. Royal Society Open Science 1:140131.

Jackson, R.R., X.J. Nelson & G.O. Sune. 2005. A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. Proceedings of the National Academy of Sciences (USA) 102:15155–15160.

Kamil, A.C. & A.B. Bond. 2006. Selective attention, priming, and foraging behavior. Pp. 106–126. *In* Comparative Cognition: Experimental Explorations of Animal Intelligence. (E.A. Wasserman & T.R. Zentall, eds.). Oxford University Press, New York.

Kennedy, J.S. 1992. The New Anthropomorphism. Cambridge University Press, Cambridge.

Konishi, M. 1965. The role of auditory feedback in the control of vocalisation in the white-crowned sparrow. Zeitschrift fuer Tierpsychologie 22:770–778.

Kovac, D. & B. Streit. 1996. The arthropod community of bamboo internodes in Peninsular Malaysia: microzonation and trophic structure. Pp. 85–99. *In* Tropical Rainforest Research — Current Issues. (D.S. Edwards, W.E. Booth & S.C. Choy, eds.). Kluwer Academic Publishers, Dordrecht.

Kruuk, H. 2003. Niko's Nature: A Life of Niko Tinbergen and his Science of Animal Behaviour. Oxford University Press, Oxford.

Kuja, J.O., R.R. Jackson, G.O. Sune, R.N.H. Karanja, Z.O. Lagat & G.E. Carvell. 2012. Nectar meals of a mosquito-specialist spider. Psyche 2012:898721.

Laird, M. 1947. A ceratopogonine midge (*Culicoides anophelis* Edwards, 1922) sucking engorged blood from a mosquito (*Armigeres lacuum* Edwards, 1922) at Palmalmal, New Britain. Transactions and Proceedings of the Royal Society of New Zealand 76:158–161.

Laland, K.N., F.J. Odling-Smee & M.W. Feldman. 1996. The evolutionary consequences of niche construction: a theoretical investigation using two-locus theory. Journal of Evolutionary Biology 9:293–316.

Land, M.F. 1969a. Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. Journal of Experimental Biology 51:443–470.

Land, M.F. 1969b. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. Journal of Experimental Biology 51:471–493.

Land, M.F. 1971. Orientation by jumping spiders in the absence of visual feedback. Journal of Experimental Biology 54:119–139.

Land, M.F. & D.-E. Nilsson. 2012. Animal Eyes, 2nd ed. Oxford University Press, Oxford.

Lehane, M.J. 2005. The Biology of Blood-sucking in Insects, 2nd ed. Cambridge University Press, New York.

Lettvin, J.Y., H.R. Maturana, W.S. McCulloch & W.H. Pitts. 1959. What the frog's eye tells the frog's brain. Proceedings of the Institute of Radio Engineers 47:1940–1951.

Levins, R. 1968. Evolution in Changing Environments. Princeton University Press, Princeton.

Lorenz, K. 1965. Evolution and Modification of Behavior. University of Chicago Press, Chicago.

Ma, Y., J. Xu, Z. Yang, X. Wang, Z. Lin & W. Zhao, et al. (2013). A video clip of the biting midge *Culicoides anophelis* ingesting blood from an engorged *Anopheles* mosquito in Hainan, China. Parasites & Vectors 6:326.

Maimusa, A.H., S. Rabiu, M.N. Inusa & M.M. Grandawa. 2012. Prey preferences of *Evarcha flavocincta* and *Plexippus petersi* (Araneae: Salticidae) from Malaysia. Asian Journal of Experimental Biological Sciences 3:105–109.

Mandler, G. 2013. The limit of mental structures. Journal of General Psychology 140:243–250.

Marler, P. 1952. Variations in the song of the chaffinch, *Fringilla coelebs*. Ibis 94:458–472.

Mathis, C. & L. Berland. 1933. Une araigneé africaine: *Plexippus paykulli*, enemie naturelle des *Stegomyia* hotes des maisons. Comptes Rendus de l'Académie des Sciences Paris 197:271–272.

Mayntz, D., D. Raubenheimer, M. Salomon, S. Toft & S.J. Simpson. 2005. Nutrient-specific foraging in invertebrate predators. Science 307:111–113.

Mousseau, T.A. & C.W. Fox. 1998. Maternal Effects as Adaptations. Oxford University Press, New York.

Mukabana, W.R., W. Takken, R. Coe & B.G.J. Knols. 2002. Host-specific cues cause differential attractiveness of Kenyan men to the African malaria vector *Anopheles gambiae*. Malaria Journal 1:17.

Murray, C.J., L.C. Rosenfeld, S.S. Lim, K.G. Andrews, K.J. Foreman & D. Haring, et al. (2012). Global malaria mortality between 1980 and 2010: a systematic analysis. Lancet 379:413–431.

Nandi, N.C. & S.K. Raut. 1985. Predatory behaviour of the pholcid spider *Crossopriza lyoni* (Blackwall) on mosquitoes (*Aedes* sp.). Bulletin of the Zoological Survey of India 7:179–183.

Nelson, X.J. & R.R. Jackson. 2006. A predator from East Africa that chooses malaria vectors as preferred prey. PLOS One 1:e132.

Nelson, X.J. & R.R. Jackson. 2011. Flexibility in the foraging strategies of spiders. Pp. 31–56. *In* Spider Behaviour: Flexibility and Versatility. (M.E. Herberstein, ed.). Cambridge University Press, Cambridge.

Nelson, X.J. & R.R. Jackson. 2012a. Fine tuning of vision-based prey-choice decisions by a predator that targets malaria vectors. Journal of Arachnology 40:23–33.

Nelson, X.J. & R.R. Jackson. 2012b. The discerning predator: decision rules underlying prey classification by a mosquito-eating jumping spider. Journal of Experimental Biology 215:2255–2261.

Nelson, X.J. & R.R. Jackson. 2013. Hunger-driven response by a nectar-eating jumping spider to specific phytochemicals. Chemoecology 23:149–153.

Nelson, X.J., R.R. Jackson & G.O. Sune. 2005. Use of *Anopheles*-specific prey-capture behavior by the small juveniles of *Evarcha culicivora*, a mosquito-eating jumping spider. Journal of Arachnology 33:541–548.

Nelson, X.J., A.J. Pratt, X. Cheseto, B. Torto & R.R. Jackson. 2012. Mediation of a plant-spider association by specific volatile compounds. Journal of Chemical Ecology 38:1081–1092.

Njiru, B.N., W.R. Mukabana, W. Takken & B.G.J. Knols. 2006. Trapping of the malaria vector *Anopheles gambiae* with odour-baited MM-X traps in semi-field conditions in western Kenya. Malaria Journal 5:39.

Omolo, M.O., B. Njiru, I.O. Ndiege, R.M. Musau & A. Hassanali. 2013. Differential attractiveness of human foot odours to *Anopheles gambiae* Giles sensu stricto (Diptera: Culicidae) and variation in their chemical composition. Acta Tropica 128:144–148.

Packard, R.M. 2007. The Making of a Tropical Disease: A Short History of Malaria. Johns Hopkins University Press, Baltimore, Maryland.

Pashler, H.E. 1998. The Psychology of Attention. MIT Press, Cambridge, Massachusetts.

Pekár, S. & S. Toft. In press. Trophic specialisation in a predatory group: the case of prey-specialised spiders (Araneae). Biological Reviews of the Cambridge Philosophical Society.

Perevozkin, V.P., S.V. Lukyantsev & M.I. Gordeev. 2004. Comparative analysis of foraging behavior in aquatic and semiaquatic spiders of the genera *Argyroneta*, *Dolomedes*, *Pirata*, and *Pardosa*. Russian Journal of Ecology 35:103–109.

Perez-Tris, J., D. Hasselquist, O. Hellgren, A. Krizanauskiene, J. Waldenström & S. Bensch. 2005. What are malaria parasites? Trends in Parasitology 21:209–211.

Pietrewicz, A.T. & A.C. Kamil. 1979. Search image formation in the blue jay (*Cyanocitta cristata*). Science 204:1332–1333.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics 15:523–575.

Pylyshyn, Z.W. 2003. Return of the mental image: are there really pictures in the brain? Trends in Cognitive Sciences 7:113–118.

Ramoska, W.A. & R.A. Sweet. 1981. Predation on mosquitoes (Diptera: Culicidae) breeding in tires by the spider *Agelenopsis naevia* (Araneae: Agelenidae). Journal of Medical Entomology 18:355–356.

Řezáč, M., S. Pekár & Y. Lubin. 2008. How oniscophagous spiders overcome woodlouse armour. Journal of Zoology 275:64–71.

Riechert, S.E. & T. Lockley. 1984. Spiders as biological control agents. Annual Review of Entomology 29:299–320.

Roff, D.A. & D.J. Fairbairn. 2007. The evolution of trade-offs: where are we? Journal of Evolutionary Biology 20:433–447.

Roitberg, B.D., E.B. Mondor & J.G.A. Tyerman. 2003. Pouncing spider, flying mosquito: blood acquisition increases predation risk in mosquitoes. Behavioral Ecology 14:736–740.

Rouder, J.N., R.D. Morey, N. Cowan, C.E. Zwilling, C.C. Morey & M.S. Pratte. 2008. An assessment of fixed-capacity models of visual working memory. Proceedings of the National Academy of Sciences (USA) 105:5975–5979.

Royama, T. 1970. Factors governing the hunting behavior and selection of food by the great tit (*Parus major* L.). Journal of Animal Ecology 39:619–668.

Sagi, D. 2011. Perceptual learning in *Vision Research*. Vision Research 51:1552–1566.

Service, M.W. 1973. Mortalities of the larvae of the *Anopheles gambiae* Giles complex and detection of predators by the precipitin test. Bulletin of Entomological Research 62:359–369.

Shanks, D.R. 2010. Learning: from association to cognition. Annual Review of Psychology 61:273–301.

Shettleworth, S.J. 2010. Cognition, Evolution, and Behavior, 2nd ed. Oxford University Press, New York.

Sinka, M.E., M.J. Bangs, S. Manguin, M. Coetzee, C.M. Mbogo & J. Hemingway, et al. (2010). The dominant *Anopheles* vectors of human malaria in Africa, Europe and the Middle East: occurrence data, distribution maps and bionomic précis. Parasites & Vectors 3:117.

Spielman, A. & M. D'Antonio. 2001. Mosquito: a Natural History of Our Most Persistent and Deadly Foe. Hyperion, New York.

Stearns, S.C. 1989. Trade-offs in life-history evolution. Functional Ecology 3:259–268.

Stouffer, D.B., J. Camacho, W. Jiang & L.A. Amaral. 2007. Evidence for the existence of a robust pattern of prey selection in food webs. Proceedings of the Royal Society Series B 274:1931–1940.

Strickman, D., R. Sithiprasasna & D. Southard. 1997. Bionomics of the spider, *Crossopriza lyoni* (Araneae, Pholcidae), a predator of dengue vectors in Thailand. Journal of Arachnology 25:194–201.

Sulaiman, S., B. Omar, S. Omar, I. Ghauth & J. Jeffery. 1990. Detection of *Aedes aegypti* (L.) (Diptera: Culicidae) predators in urban slums in Malaysia using the precipitin test. Mosquito Borne Diseases Bulletin 7:123–126.

Sulaiman, S., Z.A. Pawanchee, M.A. Karim, J. Jeffery, V. Busparani & A. Wahab. 1996. Serological identification of the predators of adult *Aedes albopictus* (Skuse) (Diptera: Culicidae) in rubber plantations and a cemetery in Malaysia. Journal of Vector Ecology 21:22–25.

Symondson, W.O., K.D. Sunderland & M.H. Greenstone. 2002. Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47:561–594.

Takken, W. & B.G.J. Knols. 1999. Odor-mediated behavior of Afrotropical malaria mosquitoes. Annual Review of Entomology 44:131–157.

Thompson, R.M., U. Brose, J.A. Dunne, R.O. Jr. Hall, S. Hladyz & R.L. Kitching, et al. (2012). Food webs: reconciling the structure and function of biodiversity. Trends in Ecology and Evolution 27:689–697.

Tinbergen, L. 1960. The natural control of insects in pine woods I. Factors influencing the intensity of predation by songbirds. Archives Neerlandaises de Zoologie 13:265–343.

Tinbergen, N. 1951. The Study of Instinct. Clarendon Press, Oxford.

Treisman, A. 1986. Features and objects in visual processing. Scientific American 255:114–125.

Treisman, A.M. & G. Gelade. 1980. A feature integration theory of attention. Cognitive Psychology 12:97–136.

Vamosi, J.C., W.S. Armbruster & S.S. Renner. 2014. Evolutionary ecology of specialization: insights from phylogenetic analysis. Proceedings of the Royal Society B 281:20142004.

Vetter, R.S. 2013. Arachnophobic entomologists: when two more legs makes a big difference. American Entomologist 59:169–175.

Vetter, R.S. 2015. The Brown Recluse Spider. Cornell University Press, Ithaca.

von Uexküll, J. 1934. Streifzüge durch die Umwelten von Tieren und Menschen. Springer, Berlin.

Wasserman, E.A. 1997. The science of animal cognition: Past, present, and future. Journal of Experimental Psychology: Animal Behavior Processes 23:123–135.

Watanabe, T. & Y. Sasaki. 2015. Perceptual learning: toward a comprehensive theory. Annual Review of Psychology 66:197–221.

Wesolowska, W. & R.R. Jackson. 2003. *Evarcha culicivora* sp. nov., a mosquito-eating jumping spider from East Africa (Araneae: Salticidae). Annales Zoologici 53:335–338.

West-Eberhard, M.J. 2003. Developmental Plasticity and Evolution. Oxford University Press, New York.

Weterings, R., C. Umponstira & H.L. Buckley. 2014. Predation on mosquitoes by common Southeast Asian house-dwelling jumping spiders (Salticidae). Arachnology 16:122–127.

White, G.B. 1974. *Anopheles gambiae* complex and disease transmission in Africa. Transactions of the Royal Society of Tropical Medicine and Hygiene 68:278–298.

Whitlock, M.C. 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. American Naturalist 148 (Supplement): S65−S77.

Wise, D.H. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge.

Żabka, M. & D. Kovac. 1996. *Paracyrba wanlessi* — a new genus and species of Spartaeinae from Peninsular Malaysia with notes on its biology (Arachnida: Araneae: Salticidae). Senckenbergiana Biologica 76:153–161.

Zurek, D.B. & X.J. Nelson. 2012. Hyperacute motion detection by the lateral eyes of jumping spiders. Vision Research 66: 26–30.

Zurek, D.B., A.J. Taylor, C.S. Evans & X.J. Nelson. 2010. The role of the anterior lateral eyes in the vision-based behaviour of jumping spiders. Journal of Experimental Biology 213:2372–2378.

Manuscript received 8 April 2015, revised 4 May 2015.