A chemically mediated trade-off between predation risk and mate search in newts

JASON R. ROHR & DALE M. MADISON

Department of Biological Sciences, State University of New York at Binghamton

Previous studies have demonstrated that adult male red-spotted newts, *Notophthalmus viridescens*, are attracted to female sexual pheromones and avoid conspecific alarm substances that signal predation. In this study, we tested the response of red-spotted newts to different concentrations and combinations of macerated male newt extract (MNE) and gravid female odour in the laboratory and field. In the laboratory, males decreased their activity in response to MNE and showed an intermediate attraction (a trade-off) to female odour when paired with MNE. The intermediate attraction indicates that predators may inhibit mate search, and that male newts apparently take greater risks during the breeding season. Results from tests conducted at two sites within the same pond complex demonstrated plasticity in response to MNE. One site showed the laboratory trade-off between mate search and predator avoidance for males, while at the second site, no significant avoidance of MNE was detected for either sex. To explain the discrepancy in MNE avoidance between the sites we propose a trade-off that incorporates risk and resource sensitivity.

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Many animals use chemicals from their own and other species to regulate and optimize response patterns. Some of these may be attractive, such as those from prey and mates (Liley 1982; Dawley 1984a, b; Lima & Dill 1990), while others may warn individuals of nearby predators (Lima & Dill 1990). It is common for these chemicals to induce conflicting responses, requiring behavioural trade-offs (Kats & Dill 1998). For example, in predator–prey interactions, prey often compromise feeding, courting and territorial defence to avoid predators (Dill 1987; Petranka 1989; Skelly & Werner 1990; Bishop & Brown 1992; Forsgren & Magnhagen 1993; Candolin 1997).

In conflicts where two demands cannot be satisfied simultaneously, the threat sensitivity hypothesis (Helfman 1989) and optimality theory (Miliniski & Heller 1978; Sih 1980) predict a trade-off between the threat a predator imposes and the needs of the prey. Both concepts submit that natural selection should favour organisms that take action appropriate to the magnitude of threat, rather than giving up feeding and mating opportunities in response to all predators. Threat-sensitive decision making can be complex since prey may differ in boldness (Wilson et al. 1993), and since predation threat may vary over time and between predators (Helfman 1989; Bishop & Brown 1992).

The few studies to investigate risk-sensitive reproductive behaviours have shown that predators can alter the courting, mating and mate choice of prey (Forsgren 1992; Berglund 1993; Forsgren & Magnhagen 1993; Hedrick & Dill 1993; Godin 1996; Candolin 1997; see fish review by Sih 1994). However, almost no studies have examined the effects of predators on mate search (Sih 1994). The emphasis on courtship and mating rather than mate search is surprising, since mate search has been shown to increase predation risk (Moore 1987; Magnhagen 1991), and is often a prerequisite to courting and mating. For this reason, we examined risk-sensitive mate search in aquatic, eastern red-spotted newts, *Notophthalmus viridescens*.

Aquatic environments may present challenges to successful mate search and predator identification. Dense vegetation and turbidity can make visual cues in aquatic habitats unreliable, often favouring chemical detection of predators and conspecifics (Dodson et al. 1994; Kats & Dill 1998). Discerning chemical concentrations may be required to make appropriate decisions regarding predation risk and mate search, since the potency of an odour may provide information about the distance or number of predators and mates. Few studies, however, have shown that prey increase their response to higher concentrations of predator chemical cues or prey alarm pheromones associated with predation (but see Petranka

Correspondence: D. M. Madison, Department of Biological Sciences, State University of New York at Binghamton, Binghamton, NY 13902-6000, U.S.A. (email: dmadison@binghamton.edu).

1989; Loose & Dawidowicz 1994; Horat & Semlitsch 1994; McKelvey & Forward 1995).

Recently, adult eastern red-spotted newts were shown to avoid chemicals from injured conspecifics but not those from heterospecific salamanders, which was hypothesized as a predator avoidance behaviour (Marvin & Hutchinson 1995; Woody & Mathis 1997). Adult males are also attracted to pheromones released from gravid females (Dawley 1984a), and newts reduce their activity when exposed to a predator stimulus in the field and laboratory (Ducey & Dulkiewicz 1994). The purpose of our study was to use different concentrations and combinations of conspecifc alarm chemicals and gravid female odour to corroborate chemically mediated predator avoidance and mate attraction in newts, and then to determine whether newts make trade-offs between predator avoidance and mate search, as hypothesized by optimality and threat sensitivity theories. We predicted that conspecific alarm chemicals would reduce newt activity and elicit an avoidance response in male newts, and that female scent would attract males. We expected conspecific alarm substance combined with female odour to be significantly less repulsive than the alarm substance alone, but significantly more repulsive than female odour alone. Finally, we hypothesized that the intermediate concentration of alarm substance would induce significantly less avoidance than the most concentrated extract, and significantly more avoidance than the least concentrated extract.

MATERIALS AND METHODS

Laboratory Experiment

We collected adult eastern red-spotted newts from a private pond in Chenango County, New York, U.S.A. in early autumn of 1998. We separated the newts by sex and placed them in cattle troughs containing 567 litres of aged tap water, with no more than 40 same-sex newts per tank. We maintained the tanks in a controlled environment chamber at 18 °C on a 14:10 h light:dark cycle. Simulated vegetation was placed in each tank. We fed the newts a liberal diet of chopped earthworms and freeze-dried blood worms every week.

Test troughs consisted of white, U-shaped, gutters 101 cm long (11.4 × 6.4 cm) sealed at both ends with plastic caps. We marked the insides of the gutters with three cross lines that created four equal subdivisions.

We made rectangular release cages (21 × 7.6 × 6.4 cm) by sewing together clear, perforated plastic normally used for needlepoint (2-mm square holes). We covered the top and two longest sides of the cages with grey tape to discourage climbing. Each cage was centred in the trough with the longest axis of the cage bisecting the midline of the trough. We filled each gutter with 3.5 litres of aged tap water at 20 °C and placed clear plastic over each trough on either side of the cage to isolate the system from air movements in the testing room.

Experiments began 2 days after the newts were collected. We arbitrarily chose 12 males in breeding condition from the source population. We used a random number table to randomize the placement of each newt in the 12 numbered troughs, with the stipulation that no animal could be exposed to the same treatment more than once. We then allowed the newts to habituate in the release cages for 75 min before adding test substances (see below) to the trough ends. This habituation period appeared to be sufficient since, in most cases, newt movement did not appear frenetic or absent.

Test substances included alarm and female odours. We prepared and froze alarm chemicals according to Woody & Mathis (1997), with the exception that we collected the alarm substance by macerating entire male newts rather than only newt skin in an attempt to simulate more closely a natural predation event. We thawed the alarm substance just before use. To collect female pheromone, we placed two of the largest captive females (both 52 mm, snout–posterior vent) in a bowl filled with 600 ml of aged tap water 2 days before the experiment. Samples of this water served as the female pheromone stimulus. We chose these females because female length is positively correlated with fecundity (Verrell 1986), and thus, we hypothesized that larger females would signal more strongly than smaller ones.

We made four different test solutions, 9 ml each, using combinations of the alarm and female odours above: female odour combined with macerated male newt extract (F+MNE), macerated male newt extract alone (MNE), female odour alone (F), and a control treatment of only aged tap water (C). All solutions were prepared with 3 ml of alarm chemical, 6 ml of female rinse water, and, if necessary, aged tap water to bring the test solution to 9 ml. We assumed that female rinse was less potent than MNE, and therefore used more female odour than MNE in our test solutions.

We assigned test solutions to one end of each trough (right or left) by stratified randomization, and assigned 9 ml of water to the opposite end. The test solution or water was slowly pipetted at the appropriate ends of the troughs through a small hole in the plastic cover. Since we ran 12 troughs concurrently, three replicates of the four treatments were run each day for 10 straight days.

We began trials by slowly lifting the cages above each newt 5 min after we injected the test solution. We subsequently stood as motionless as possible recording the quadrant that each newt occupied at 1-min intervals for 30 min. Newt behaviour in the presence and absence (using video) of an observer did not appear to differ. We compared quadrant location relative to the test solution and the number of lines crossed (activity) for all four treatments using Kruskal–Wallis tests. We did not predict how male activity would change in response to female scent, and so, unlike all other tests, these were two-tailed. The family of contrasts was determined by variance sources (female and MNE), and the alpha level was adjusted using the Bonferroni t procedure (Sokal & Rohlf 1998).

Field Experiment

Unless otherwise stated, we used a minnow-trap based experimental design for our field studies (Woody &

Mathis 1997). Field treatments were identical to the laboratory treatments except for the addition of an intermediate alarm chemical concentration and its combination with female odour. We tested alarm substance solutions of 100, 50, and 0% MNE by placing 5 ml on a cellulose sponge ($1 \times 2.5 \times 4$ cm), and then placing the sponge in the appropriate trap. Deviations from Woody & Mathis (1997) were as follows. The female scent was supplied by placing a large female from our laboratory population into the appropriate trap. As previously mentioned, entire male newts rather than just skin were used to obtain the conspecific alarm chemical. We also placed 24 traps a minimum of 12.5 m apart (rather than 1 m apart) along various shores of Binghamton University's Nature Preserve in Broome County, New York. The larger trap spacing reduced possible treatment effects between traps. Finally, all trapping occurred daily during April 1999 between 1100 and 1500 hours, and traps were left open without treatment at all other times.

To diversify trap placement in the Nature Preserve Pond complex, we placed 13 traps along the shore of the main pond and 11 in a secondary side pool. The two sites were only separated by a beaver dam and were thus considered to contain a single newt population.

We assigned treatments in the field using a stratified randomization process. As we visited each of the 24 traps sequentially, we randomly assigned the six treatments with the stipulation that each treatment must be assigned to a trap before any treatment could be assigned to a second trap. This process produced a complete set of treatments for the first six traps, and four such sets within the 24 traps. We repeated this procedure on subsequent days with two modifications. First, within each successive set of six traps, each treatment was assigned to a different trap. Second, on every third day, we did not assign any treatments, but set and checked the traps as a 'nontreatment control' (traps containing a sponge without MNE or a female during a treatment period were considered 'treatment controls'). We continued this daily process until every trap received each treatment once, which required 6 treatment days and 3 nontreatment days. After this 9-day experimental period, we waited a day and then repeated the entire process. Since most males are actively searching for receptive females during the breeding season and our sites seemed to contain relatively dense newt populations, significant pseudoreplication was unlikely.

During daily trap checks, we counted the number of males and females caught in each trap, minus introduced females, 2 h after traps were set. Two traps in the main pond did not catch any newts during the experiment, and since each contributed a zero to all treatment groups (and nontreatment controls), we excluded these traps from the analyses. Therefore, the total experiment produced 22 trap-days for each treatment (11 traps $\times$ 2 replicates) and 77 trap-days for the nontreatment controls (3 days $\times$ 2 replicates+first day of experiment). We used Wilcoxon matched-pairs signed-ranks (T) and Friedman (χ_2^2) tests to examine for treatment effects, and Mann–Whitney U tests to analyse for site effects. Since a newt entering a trap could attract other newts, and therefore inflate differences between treatment groups, we used a chi-square

test to compare the number of traps containing newts for the three MNE treatments to test for conspecific attraction. Since Woody & Mathis found no social facilitation in their study, we predicted no conspecific attraction. We applied the same hypotheses used in the laboratory experiment to the field experiment. We also calculated the power (Π) of statistical tests for nonsignificant results when deemed helpful for data interpretation (Lehmann 1975).

Ethical Note

All methods adhered to the *Guidelines for the Use of Animals in Research*. This study was licensed through the New York State Department of Environmental Conservation (LCP97-256, LCP98-427) and approved by the State University of New York at Binghamton (Institutional Animal Care and Use Committee, Protocol Nos 406-98, 467-00). We chose to decapitate three newts to obtain conspecific alarm chemicals since this was the same number used by Woody & Mathis (1997), and therefore facilitates result comparisons.

RESULTS

Laboratory Experiment

Six of 30 newts initially moved towards MNE alone and then became predominantly immobile for the remainder of the trials. This apparent freeze response produced variance heterogeneity and a slightly bimodal frequency distribution for the MNE treatments, requiring the use nonparametric analyses.

Male newts were attracted to F treatment (Kruskal–Wallis test: $H_{1,120}=9.75$, $P<0.01$), and avoided MNE ($H_{1,120}=5.42$, $P<0.02$). F+MNE produced an intermediate average location relative to F alone ($H_{1,60}=4.17$, $P<0.05$) and to MNE alone ($H_{1,60}=6.59$, $P<0.02$; Fig. 1a). C treatments also produced an intermediate average location relative to F ($H_{1,60}=5.64$, $P<0.02$) and MNE ($H_{1,60}=5.06$, $P<0.025$; Fig. 1a).

Newt activity decreased in response to MNE ($H_{1,120}=6.80$, $P<0.01$), but was not significantly affected by F treatment ($H_{1,120}=0.19$, $P=0.66$). In fact, F, F+MNE, and C treatments did not significantly differ in activity ($H_{2,90}=3.21$, $P=0.20$). Newts in the presence of MNE alone were significantly less active than newts exposed to C ($H_{1,60}=12.33$, $P<0.001$) and F+MNE treatments ($H_{1,60}=5.63$, $P<0.02$), and the difference between MNE and F alone was nearly significant ($H_{1,60}=3.73$, $P=0.053$; Fig. 1b).

Field Experiment

There was no significant difference between newt capture rates in traps containing 100% MNE (mean $\pm$ SE=0.91 $\pm$ 0.13), 50% MNE (mean $\pm$ SE=1.15 $\pm$ 0.15), or 0% MNE (mean $\pm$ SE=1.22 $\pm$ 0.14; chi-square test: $\chi_2^2=2.71$, $P=0.26$). However, it was immediately apparent that significantly fewer newts were captured per trap in the main pond (mean $\pm$ SE=0.45 $\pm$ 0.08) than in the side pool (mean $\pm$ SE=1.58 $\pm$ 0.17; Mann–Whitney U test:
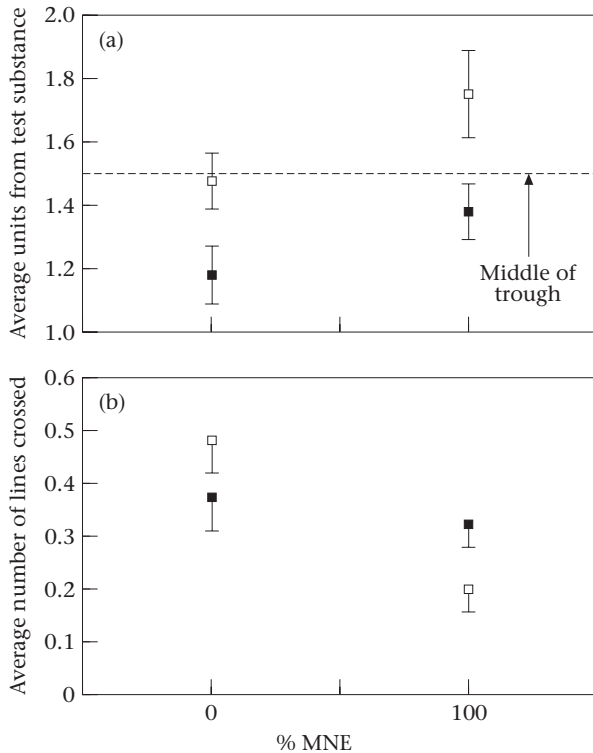
Figure 1. Avoidance (a) and activity (b) responses (per 30 min) of male newts to female odour, macerated male newt extract (MNE), control water, and their combinations in the laboratory. Symbols in (a) reflect the mean±SE distance (N=30) from the quadrant in which test solution was initially injected, and symbols in (b) reflect the associated mean±SE number of lines crossed during newt activity (N=30; see Methods). □: No female scent added; ■: female scent added.
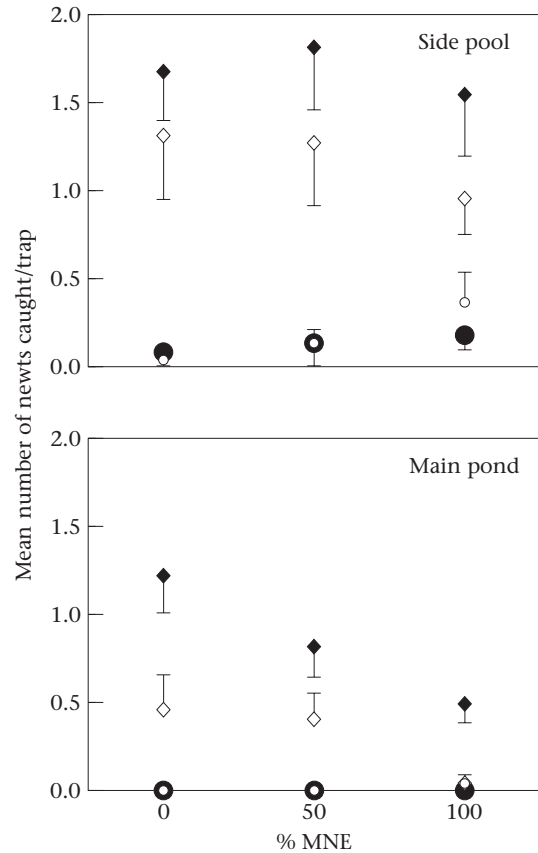

Figure 2. Mean±SE number of male (diamonds) and female (circles) newts caught per trap (N=22) containing macerated male newt extract (MNE), a laboratory female, control water, and their combinations in the side pool and main pond of Binghamton University's Nature Preserve. Open symbols: traps without a laboratory female; closed symbols: traps containing a laboratory female.

U=2810, N_1=77, N_2=22, P<0.001). Due to this difference in capture rates, we continued our analysis by statistically examining the main pond and side pool results separately.

In the main pond, male newts were attracted to F treatment (Wilcoxon matched-pairs signed-ranks test: T=234.0, N=66, P<0.001) and avoided MNE (Friedman test: χ_2^2=13.42, P<0.01; Fig. 2), as predicted. There was a perfect negative rank correlation between MNE concentration and the number of male newts caught per trap (Fig. 2). Traps containing 100% MNE caught significantly fewer male newts than those with 50% MNE (Wilcoxon matched-pairs signed-ranks test: T=50.0, N=44, P<0.0125) or 0% MNE (T=24.0, N=44, P<0.001; Fig. 2); however, 50% MNE treatments were not significantly different from 0% MNE treatments (T=68.0, N=44, P=0.17, Π=0.05). This nonsignificant result was strongly influenced by the lack of difference between 50% MNE and C treatments (T=22.5, N=22, P=1.00, Π=0.07; Fig. 2). Traps with F+100% MNE caught significantly fewer male newts than traps with F treatment alone (T=18.0, N=22, P<0.01), and significantly more male newts than traps with 100% MNE alone (T=6.5, N=22, P<0.01; Fig. 2). The same pattern existed for traps with F+50% MNE versus traps with F treatment alone (T=13.5, N=22, P=0.08) and 50% MNE alone (T=36.0, N=22, P=0.10; Fig. 2), although

both analyses were marginally nonsignificant. No statistical tests were run on female capture rates in the main pond because only one female was captured in traps containing treatments; this female being in a trap with only 100% MNE.

Conspecific attraction did not inflate differences between treatment groups in the main pond. Twenty-three of 44 traps with 0% MNE (C+F) captured newts compared to 21 of 44 traps with 50% MNE (50% MNE+F+50% MNE; chi-square test: χ_2^2=0.18, P=0.67) and 13 of 44 traps with 100% MNE (100% MNE+F+100% MNE; χ_2^2=4.70, P<0.05). Traps with 0% MNE and 50% MNE captured zero to three newts per trap, and 100% MNE traps caught zero to one newt per trap.

In the side pool, male newts were attracted to traps with F treatment (Wilcoxon matched-pairs signed-ranks test: T=327.0, N=66, P<0.02), but did not avoid traps with MNE (Friedman test: χ_2^2=0.19, P=0.91; Fig. 2). There was no significant difference in male capture rates between the three MNE treatments containing laboratory females (chi-square test: χ_2^2=0.08, P=0.96) or the three MNE treatments lacking laboratory females (χ_2^2=0.13, P=0.94; Fig. 2). The failure to detect MNE avoidance, however, does not indicate that side pool newts were not avoiding MNE.

Social facilitation did not inflate differences between treatment groups in the side pool. Thirty-three of 44 traps with 0% MNE (C+F) captured newts compared to 32 of 44 traps with 50% MNE (50% MNE+F+50% MNE; chi-square test: $\chi^2_2=0.06$, $P=0.81$), and 32 of 44 traps with 100% MNE (100% MNE+F+100% MNE; $\chi^2_2=0.06$, $P=0.81$). Traps with 0, 50 and 100% MNE all captured zero to six newts per trap.

The response of females to MNE remains uncertain. Twelve females were captured in nine traps containing 100% MNE (4 in F+100% MNE, 8 in 100% MNE alone; Fig. 2b), while 15 females were captured in 15 of 99 control traps (treatment+nontreatment). The null hypothesis was rejected when comparing 100% MNE to the 99 control traps (binomial test: $P<0.02$), but was not rejected after removing the effect of conspecific attraction by comparing the five 100% MNE traps that captured females to the 15 control traps that captured females (binomial test: $P=0.14$).

Because captured females could increase the concentration of female sexual pheromones and therefore elevate male capture rates, we reanalysed the data from both sites after excluding traps where females were captured. When we removed traps that captured females, no trends changed and no probability values crossed the alpha significance threshold. It is also possible that treatment effects could have lasted for more than 24 h; however, this was unlikely because there was no significant difference in the main pond between the number of nontreatment control traps (out of the 11) that captured newts, which were located where either 100% MNE, female, or control traps were the day before.

DISCUSSION

Our finding that males were attracted to female odour and avoided 100% MNE in the laboratory and main pond were consistent with the results of Dawley (1984a), Marvin & Hutchinson (1995) and Woody & Mathis (1997). Reduced activity to 100% MNE alone in the laboratory was consistent with the results of Ducey & Dulkiewicz (1994), who demonstrated that adult terrestrial red-spotted newts decrease their activity in response to a predator stimulus. In addition, both the crested newt, *Triturus cristatus*, and smooth newt, *Triturus vulgaris*, decrease their activity in response to conspecific extracts (Margolis 1985).

Decreased activity is also consistent with other amphibian responses to predators or cues associated with predation risk (Lawler 1989; Skelly & Werner 1990; Werner 1991; Skelly 1992; Stauffer & Semlitsch 1993). Skelly (1994) demonstrated that higher activity levels produced elevated predation rates in *Hyla versicolor* tadpoles, and suggested that increased activity raised the probability of being detected or encountered by predators. Since many potential newt predators rely on visual cues while searching for prey (birds: Howard & Brodie 1973; fish: Dixon & Baker 1988), and since adult newts are cryptically coloured, decreased activity is probably an appropriate antipredatory response. In addition, numerous prey responses to alarm signals have been shown to increase prey survivorship (Hews 1988; Mathis & Smith 1993; Wisenden et al. 1999), and we suspect that the newt response is not an exception.

Although avoidance of MNE could be explained by aversion to conspecific social pheromones rather than antipredatory alarm substances, multiple newt captures per trap recorded by Woody & Mathis (1997) and in this study (10 and 7, respectively) are inconsistent with newts avoiding one another's scent. In addition, we have demonstrated that males are attracted to groups of multiple same-sex conspecifics during the breeding season (unpublished data).

Since avoidance of social pheromones does not seem to account for the results, the intermediate male response in both the laboratory and main pond to F+100% MNE relative to the two odours alone most probably indicates that males made a compromise between predator avoidance and mate search. Thus, predation threat (MNE) appeared to compromise newt mate search, and female presence compromised predator avoidance. Based on optimality theory, male newts probably avoided F+100% MNE in the field until the cost of predation equalled the benefit of potential reproduction, at which time they began to search for the prospective mate. Therefore, male newt response to F+MNE in the laboratory and main pond was consistent with the threat sensitivity hypothesis; it was both risk and resource sensitive. Although not significant, the intermediate capture rate of traps with 50% MNE versus 0 and 100% MNE was also consistent with threat-sensitive decision making.

We used a power analysis to determine whether the lack of MNE avoidance in the side pool was merely a product of insufficient sample size, and whether the site difference in MNE avoidance appeared to be biologically relevant. The power of our test for total and male newt avoidance of 100% MNE in the side pool was 0.03 and 0.09, respectively. Therefore, it was very probable that side pool newts did avoid 100% MNE, but the behaviour went undetected, a caution discussed by Chivers & Smith (1998) in the context of risk/resource trade-offs. For a power of 0.80 and an alpha of 0.025, we would have needed approximately 4949 traps ($\Delta=0.045$, $\sigma^2=3.86$) in the side pool to detect significant total newt avoidance and 74 traps ($\Delta=0.364$, $\sigma^2=3.67$) to reveal male newt avoidance compared with only 14 ($\Delta=0.364$, $\sigma^2=0.72$) and 10 ($\Delta=0.409$, $\sigma^2=0.63$) main pond traps, respectively (Lehman 1975). Although we cannot confidently claim that newts in the side pool were not avoiding MNE, there clearly appeared to be a site difference in response to the alarm signal and a much smaller effect size in the side pool.

This site discrepancy in response to MNE was the most surprising result, but it too can be explained by a trade-off between mate search and predator avoidance. The discrepancy could have been a product of an increased resource level (benefit), or a decreased risk level (cost) in the side pool, both of which we believe are equally parsimonious explanations.

The side pool appeared to have a lower risk level than the main pond, which could have allowed males and females to relax their avoidance of alarm substances and

to respond more to sexual pheromones in the same treatments. The side pool had characteristics that would lower predation threat, specifically a greater newt density, fewer perches for foraging birds, a smaller littoral zone, and fewer potential bird, reptile, rodent and fish predators than the main pond (Rohr & Madison, in press). Although many fish may be attracted to the odour of dead animals, fish were not attracted to traps with MNE at either site, nor did adult newts avoid traps with fish (Rohr & Madison, in press).

This observed plasticity in response to MNE might be critical for adult newts since they frequently encounter multiple habitats with varying population densities and predation regimes. Predation threat can vary as adults migrate between ponds (Miaud et al. 1993), travel to and from terrestrial refuges during late summer months, and leave the pond to seek terrestrial overwintering hibernacula (Hurlbert 1969). Marvin & Hutchinson (1995) demonstrated that adult newts avoid conspecific skin extracts in semiterrestrial petri dishes, suggesting that these alarm chemicals may be effective in both aquatic and terrestrial habitats. Newts can also live for up to 13 years (Caetano & Leclair 1996), in which time predation pressures within a pond complex could fluctuate dramatically. Due to expected inter- and intrahabitat variation, it is not surprising that newts appear to be able to estimate local predation pressures and to respond accordingly.

It seems equally possible that a more abundant resource, specifically the higher number of females in the side pool, was somehow responsible for the avoidance discrepancy between the sites. Like the laboratory females placed in traps, the greater number of resident females in the side pool could have compromised male avoidance of MNE, making it extremely difficult to find significant avoidance after 2 h. If females elevate the activity of males in the presence of 100% MNE, as our laboratory data suggest, it could have increased male encounter rates with, and thus capture rates in, our MNE traps.

This greater quantity of females in the side pool, coupled with the possibility that females are attracted to MNE, may have offset male MNE avoidance, producing the site discrepancy. Male newts of both *Cynops* and *Triturus* genera release female-enticing chemicals (see review in Kikuyama et al. 1999), and therefore it is possible that MNE contained both alarm and female-attracting substances. Females, like the males, then could have made a trade-off between the conflicting demands of predator avoidance and the increased probability of mate choice and reproduction.

Female attraction to MNE cannot fully explain the results because removing traps that captured females from our analyses failed to produce male MNE avoidance in the side pool, and females were not significantly attracted to MNE after removing the effect of conspecific attraction. Furthermore, subsequent field studies failed to show female attraction to MNE during the breeding season (J. R. Rohr, unpublished data). However, these studies also failed to demonstrate female MNE avoidance. Female response to MNE and its potential consequences on newt mate search and population dynamics clearly requires further investigation.

The main pond and laboratory results provide the more cogent evidence for a male trade-off between mate search and predator avoidance, but the side pool data seem to support this trade-off for both sexes. Deliberately increasing predation risk in an attempt to increase mate encounter probabilities may maximize gene propagation, and thus, may be an optimal newt fitness strategy. Future research should quantify how trade-offs between reproduction and predator avoidance affect individual fitness in ecological time.

Acknowledgments

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