ÉCOSCIENCE

5 (3) : 361-394 (1998)

The scent of death: Chemosensory assessment of predation risk by prey animals[1]

Lee B. KATS, Natural Science Division, Pepperdine University, Malibu, California 90263, U.S.A.
Lawrence M. DILL, Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Colombia V5A 1S6, Canada.

Abstract: It is well documented that animals take risk of predation into account when making decisions about how to behave in particular situations, often trading-off risk against opportunities for mating or acquiring energy. Such an ability implies that animals have reliable information about the risk of predation at a given place and time. Chemosensory cues are an important source of such information. They reliably reveal the presence of predators (or their presence in the immediate past) and may also provide information on predator activity level and diet. In certain circumstances (*e.g.*, in the dark, for animals in hiding) they may be the only cues available. Although a vast literature exists on the responses of prey to predator chemosensory cues (or odours), these studies are widely scattered, from marine biology to biological control, and not well known or appreciated by behavioural ecologists. In this paper, we provide an exhaustive review of this literature, primarily in tabular form. We highlight some of the more representative examples in the text, and discuss some ecological and evolutionary aspects of the use of chemosensory information for prey decision making. Curiously, only one example illustrates the ability of birds to detect predator odours and we have found no examples for terrestrial insects, suggesting a fruitful area for future study.
Keywords: predator-prey, chemical cues, antipredator behaviour, morphological defenses, life-history adaptation.

Résumé : Il est bien connu qu'un animal qui doit prendre une décision d'ordre comportemental prend en considération le risque de prédation associé à cette décision. Souvent, l'animal passera outre ce risque pour se reproduire ou se nourrir. Une telle habilité implique que l'animal a une information spatio-temporelle valable sur le risque de prédation. Les indices chimiques constituent une source importante d'informations. Ils révèlent la présence de prédateurs (où leur passage récent) et donnent des renseignements sur le taux d'activité du prédateur et sur sa diète. Dans certaines circonstances (dans l'obscurité ou en présence de prédateurs chassant à l'affût), les indices chimiques peuvent être les seuls permettant aux proies de détecter leurs prédateurs. Il existe une littérature abondante sur la réponse des proies aux indices chimiques (ou odeurs) fournis par les prédateurs. Ces travaux sont néanmoins disparates (leurs sujets s'étendent de la biologie marine au contrôle biologique), peu connus et peu appréciés des écologistes spécialistes de l'étude des comportements. Dans cet article, nous faisons une revue exhaustive de cette littérature, notamment sous la forme de tableaux. Nous mettons en relief dans le texte les exemples les plus représentatifs. Nous discutons aussi des aspects écologiques et évolutifs reliés à l'utilisation des informations chimiques par les proies lors de prises de décisions. Curieusement, un seul exemple illustre l'habilité des oiseaux à la détection des odeurs des prédateurs. Nous n'avons pas trouvé d'exemple chez les insectes terrestres. Il y a donc là un terrain potentiellement fructueux pour de futurs travaux.
Mots-clés : prédateur-proie, indices chimiques, comportement anti-prédateur, défenses morphologiques, adaptation.

Introduction

Prey organisms exhibit a variety of adaptations for defending themselves from predators (Edmunds, 1974; Endler, 1986). These adaptations may be morphological (*e.g.*, spines and armour), physiological (*e.g.*, toxins), life historical (*e.g.*, delayed hatching) or behavioural (*e.g.*, hiding, fleeing). Many of these antipredator tactics have costs associated with them; therefore, they might be expected to be used only when the organism has an accurate assessment of predation risk and thus of the benefit of defense. Recent studies have begun to examine the proximate mechanisms involved in mediating predator-prey interactions, and in particular, mechanisms of risk assessment. Many antipredator adaptations are induced or mediated by a chemical cue from a predator.

Several recent reviews have looked at different aspects of chemically induced defenses. Induced defenses are exhibited in prey only after certain conditions have triggered their appearance. Havel (1987) concluded that many induced defenses are produced in response to chemicals from potential predators; no physical contact with the predator or chemicals from injured conspecifics are necessary for the induction of the defense. Harvell (1990; 1991; 1992) also noted that induced defenses are often triggered by water-borne chemical cues from predators. In addition, Harvell pointed out that most organisms with induced morphological defenses are either clonal or colonial. Dodson *et al.* (1994) reviewed the literature on non-visual communication in freshwater benthic organisms. Their review includes discussion about the importance of chemically-mediated antipredator behaviour in benthic invertebrates and amphibians. They also discuss the advantages and disadvantages of relying on chemical cues for avoiding predation in freshwater systems. Weldon (1990) reviewed chemically-mediated antipredator behaviour in vertebrates, but his review only touched briefly on the evolutionary significance of using chemical cues to detect predators. The

[1]Rec. 1996-08-13; acc. 1997-08-30.

literature on responses to predator chemicals is scattered in several scientific disciplines ranging from ecology and behaviour to pest management (see, for example, Sullivan *et al.*, 1988 for a review of the effectiveness of predator odours for controlling herbivorous pests). Defensive adaptations that are mediated via predator chemical cues occur in terrestrial, freshwater and marine habitats; this review will survey examples of these adaptations in all these realms. The tables represent all the literature that we were able to locate on the topic, while the text highlights example studies that illustrate general principles. We realize that organisms use many sensory modes to detect air- and water-borne chemicals (*e.g.*, taste, olfaction); however, in this review we will not distinguish between chemical detection mechanisms and will refer to all examples as being mediated via general chemoreception or chemosensory mechanisms. Despite the multiple sensory mechanisms available for chemical detection, we refer to predator chemicals as cues or odours throughout this paper.

Many prey are capable of accurate predation risk assessment (Lima & Dill, 1990). While most prey are capable of using multiple predator detection mechanisms (*e.g.*, visual, chemical, tactile), there appear to be significant advantages to chemical detection. In this paper we will examine: (*i*) responses to predator chemical cues, (*ii*) the diversity of prey taxa responsive to predator chemical cues, (*iii*) the evolutionary tradeoffs involved in chemical detection of predators, and (*iv*) factors influencing the effectiveness of the cue detection mechanism.

Types of responses to predator chemical cues

This review surveys literature for all responses of prey to predator chemicals. We do not consider studies that report responses of prey to alarm pheromones or cues from injured conspecifics (unless they "label" the predator, see Chivers & Smith this volume), and we only review interactions that are mediated via distant (non-contact) chemoreception. We do not include studies whose experimental design does not clearly allow the conclusion that the observed prey responses were to predator chemicals alone. Convincing evidence for response to a predator chemical cue requires that other sensory modalities (*e.g.*, mechanical, visual) have been eliminated in the experimental design. We have also tried to exclude those studies where the experimental design does not separate possible influences of predator odours from prey alarm substances. However, we have included studies where prey responses to predator cues cannot be differentiated from responses to novel cues. For example, many studies only compare responses of prey to predator cues and to control treatments (no cues). While a response to predator cues in such studies might only indicate a response to a novel cue, and not necessarily to a predator *per se*, we include them in this review because such a prey response would presumably still be adaptive. Tables I, II and III represent an exhaustive review of the existing literature on the responses of prey to chemical cues, organized taxonomically. Here we consider the various sorts of responses reported, indicating the range of taxa demonstrating them, and highlight a few specific studies of each.

MORPHOLOGICAL RESPONSES

Prey often have unusual physical characteristics when they are found coexisting with predators. These unusual characteristics can be the result of differential mortality brought about by predation pressure or they may be directly induced by the presence of the predators (Kerfoot, 1987). Several studies have indicated that predator chemicals stimulate the production of prey morphologies that inhibit predation (Table I); such chemically induced morphologies are most common in protozoans, rotifers, cladocerans and bryozoans. While unusual or extreme morphologies are often assumed to confer antipredator advantages, only a few of these studies conducted follow-up experiments on chemical induction by looking at prey survivorship when in direct contact with predators (*e.g.*, Kerfoot, 1987; Stemberger & Gilbert, 1987; Wicklow, 1988).

Although the induction of defensive morphologies by predator chemical cues seems fairly straightforward, it is sometimes difficult to rule out the role of behaviour underlying induced morphological defenses. For example, Appleton & Palmer (1988) found that water-borne cues from a predatory crab (*Cancer productus*) induce large apertural teeth on snails (*Thais* [*Nucella*] *lamellosa*). Starvation can also lead to the development of apertural teeth, so the response to predator odours may have been partially mediated through reduced foraging activity. In this situation it may be that apertural teeth are an adaptive response to predator chemicals but that the proximate explanation for the response is the reduction in feeding.

Most studies on predator induced phenotypes have focused on invertebrates; however, a recent study on fish (Brönmark & Miner, 1992) found that predators can induce altered body morphologies. Crucian carp (*Carassius carassius*) develop deeper bodies when reared with piscivourous pike (*Esox lucius*), and later studies suggested that the change in body morphology is cued by pike odours and not by vision or carp alarm substances (Brönmark, Petterson & Nilsson, 1993; Brönmark & Pettersson, 1994). However, given that the pike were being fed crucian carp in holding tanks before being moved to the test tank, dietary alarm cues were not entirely eliminated and the exact source of the chemical cue triggering the change in morphology remains unclear.

Chemical cue induced morphological defenses can apparently have costs to the organisms that produce them. The ciliate (*Euplotes octocarinatus*) could not produce morphological defenses in response to predator cues if it had been deprived of food (Wiackowski & Szkarlat, 1996). Further studies found that both the quantity and quality of food available affected the magnitude of the morphological response to predator chemical cues. Gastropods have reduced growth rates when they produce thicker than normal shells (Palmer, 1981). When bryozoans produce spines in response to predators, colonies have a 14% reduction in growth compared to colonies that do not have spines (Harvell, 1986). Chemically induced spines in *Daphnia* can also result in reduced growth rates and delayed reproduction (Walls & Ketola, 1989; Walls, Caswell & Ketola, 1991; Spitze, 1992) when compared to *Daphnia* without induced defenses. Cladocerans will reduce the size of protective

TABLE I. Morphological responses to predator odor

Prey	Predator	Response	Author
KINGDOM PROTISTA			
Protozoan *Onychodromus quadricornutus*	Cannibal giant conspecifics	Induced spines	Wicklow (1988)
Ciliate *Euplotes octocarinatus*	Predatory ciliates, esp. *Lembadion lucens*	Induced change in cell shape & size	Kuhlmann & Heckmann (1985); Jerka-Dziadosz *et al.*(1987)
E. octocarinatus	Ciliate, *Stylonychia mytilus*	Induced changes in cell size & shape (wings)	Wiackawski & Szkonlat (1996)
E. octocarinatus	*Amoeba proteus*	Increased cell width	Kusch (1993c)
E. octocarinatus	Turbellarian, *Stenostomum sphagnetorum*	Induced changes in cell size & shape (wings)	Kusch & Kuhlmann (1994)
Ciliate *Euplotes spp.*	Turbellarian, *Stenostomum sphagnetorum* Ciliates, *Lembadion spp.* Rhizopoda, *Amoeba*	Induced changes in cell size & shape (wings)	Kusch (1993a,b) Kusch & Heckmann (1992)
KINGDOM ANIMALIA			
Phylum Rotifera			
Brachionus bidentata	Rotifer *Asplanchna brightwelli*	Induced spines & large size	Pourriot (1974)
Brachionus calyciflorus	Rotifer *Asplanchna*	Induced spines in offspring	Gilbert (1967)
B. calyciflorus	Rotifer *Asplanchna*	Induced spines	Halbach (1970)
Brachionus pala	Rotifer *Asplanchna*	Induced spines	de Beauchamp (1952a,b); Gilbert (1966)
Keratella spp.	Rotifer *Asplanchna*, copepods, cladocerans & gastropod *Fasciolaria hunteria*	Induced spines in offspring	Gilbert & Stemberger (1984); Stemberger & Gilbert (1984; 1987)
Keratella tropica	*Notodiaptomus incompositus*	Induced caudal spines	Zagarese & Marinone (1992)
K. tropica	Notonectid, *Buenoa fuscipennis*	Reduced caudal spines	Zagarese & Marinone (1992)
K. tropica	Copepods & cladocerans	Increased caudal spine length	Marinone & Zagarese (1991)
Phylum Mollusca			
CLASS BIVALVIA			
Mytilus edulis	Crab, *Cancer pagurus*	Secretion of more, thicker and shorter byssal threads	Cote (1995)
CLASS GASTROPODA			
Nucella lamellosa	Crab, *Cancer*	Induced large teeth on shell	Appleton & Palmer (1988)
Atlantic dogwhelk, *Nucella lapillus*	Crab *Cancer pagurus*	Induced changes in shell thickness & apertural tooth height	Palmer (1990)
Phylum Arthropoda			
CLASS CRUSTACEA			
Cladoceran *Holopedium*	*Chaoborus obscurus*	Increased gelatin capsule size	Stenson (1987; 1988)
Bosmina	*Epischura*	Induced spines	Kerfoot (1987)
Daphnia	*Chaoborus, Notonecta*, and bluegill sunfish, *Lepomis macrochirus*	Induced helmet & spines	Dodson (1988a; 1989);
Daphnia ambigua	*Chaoborus spp.*	Induced helmet and spines in adults	Hebert & Grewe (1985)
D. ambigua	*Chaoborus flavicans*	Induced helmet spikes	Hanazato (1990; 1991a,b)
Daphnia carinata	Notonectids *Anisops* and *Enithares*	Induced crest	Grant & Bayly (1981); Barry & Bayly (1985); Barry (1994)
Daphnia cucullata	*C. flavicans*	Induced helmet	Tollrian (1990)
Daphnia galeata	*C. flavicans*	Induced helmet	Hanazato (1991c)
Daphnia lumholtzi	Bleak, *Leucaspius delineatus*	Longer helmets	Tollrian (1994)
Daphnia pulex	Phantom midge larvae *Chaoborus americanus*	Induced crest and neckteeth	Krueger & Dodson (1981); Havel (1985)
D. pulex	*C. americanus*	Induced neckteeth	Parejko & Dodson (1990); Spitze (1992); Black (1993)
D. pulex	*C. americanus* and *Mochlonyx*	Induced neckteeth	Parejko (1991)

(continued on next page)

TABLE I. (concluded)

Prey	Predator	Response	Author
D. pulex	*Chaoborus crystallinus*	Induced spines	Walls & Ketola (1989)
D. pulex	*C. crystallinus*	Induced neck spine	Walls, Caswell & Ketola (1991)
D. pulex	*C. crystallinus*	Retention of spines as adults	Vuorinen, Ketola & Walls (1989)
D. pulex	*C. flavicans, Notonecta glauca*	Induced spines in offspring	Lüning (1992)
D. pulex	*C. flavicans*	Induced neckteeth	Lüning (1994)
D. pulex	Chaoborids	Induced neckteeth	Parejko & Dodson (1991)
D. pulex	*Chaoborus*	Induced neckteeth	Schwartz (1991)
D. pulex	*C. obscuripes, C. crystallinus, Mochlonyx sp., Dytiscus, Notonecta*	Induced neckteeth	Repka, Ketola & Walls (1994)
D. pulex	*Chaoborus flavicans*	Induced neckteeth	Tollrian & von Elert (1994)
Daphnia schodleri	Notonectid, *Buenoa*	Cephalic expansion	Schwartz (1991)
Barnacle *Chthamalus anisopoma*	Gastropod *Acanthina angelica*	Change in shell shape	Lively (1986)
Phylum Bryozoa			
Membranipora membranacea	Nudibranch *Doridella steinbergae*	Induced spines	Harvell (1986; 1991; 1992)
M. membranacea	Nudibranchs	Induced spines	Harvell (1990)
Phylum Chordata, Subphylum Vertebrata			
CLASS OSTEICHTHYES			
Crucian carp *Carassius carassius*	Northern pike, *Esox lucius* (pike must be piscivorous)	Increased body depth	Brönmark, Petterson & Nilsson (1993) Brönmark & Petterson (1994)

gelatinous capsules when chemical cues from predatory *Chaoborus* disappear (Stenson, 1987). Presumably the cladocerans monitor risk carefully because large capsules are expensive to maintain.

BEHAVIOURAL RESPONSES

ESCAPE AND/OR AVOIDANCE

Approximately half of the references that report chemically-mediated antipredator behaviours consider either escape or avoidance responses in prey. When prey detect predators they do not necessarily have information about whether the predator has detected them. Normally, "escape" refers to prey leaving a high risk situation once detected and/or pursued by a predator. In this review we will use "escape" for responses where prey flee areas containing predator cues, often with increases in speed or overall activity. Avoidance responses are often seen in laboratory experiments where prey are given choices between alternative habitats or paths (in the case of y-maze experiments), *i.e.*, they may choose to occupy areas with predator cues or avoid those areas. In avoidance experiments, the choice of habitat by prey is the primary indicator of predator detection and not particular changes in prey behaviour or activity. Prey responses are highly dependent on the design of the experiment. If prey are not given options that include avoiding or escaping from the chemical cue, they might be expected to respond via induced morphologies, defensive postures, increased heart rate or breathing, or immobility. Thus, just because prey demonstrate a physiological response to predator cues in an experiment does not exclude the possibility that they would typically avoid or escape from the cues if given the opportunity.

Even organisms not immediately identified with mobility or speed are known to escape predator odours. Yentsch & Pierce (1955) reported that anemones (*Stomphia coccinea*) detach from the substrate and "swim" in response to odours from a predatory sea star (*Dermasterias sp.*). The most extensive literature on escape responses comes from studies on gastropods (Table II). Gastropods are known to use chemoreception to mediate many of their behaviours (*e.g.*, locating mates, finding food; Kohn, 1961; Audeskirk & Audeskirk, 1985). Several studies (*e.g.*, Gonor, 1964; 1966; Robertson, 1961; Snyder & Snyder, 1971) noted that snails speed their escape by rolling or "leaping"; they rapidly extend the foot from the shell, thus propelling themselves a few centimeters. Other snails respond to predator chemical cues by burying themselves in the substrate (Snyder, 1967; Phillips, 1977), or crawling out of the water that contains the predator cues (Feder, 1963; Szal, 1971; Alexander & Covich, 1991). While most studies noted that snails move away from a predator cue, Dix & Hamilton (1993) noted that marsh periwinkles (*Littoraria irrorata*) show a significant increase in crawling speed in response to chemical cues from predatory conchs (*Melongena corona*), but do not necessarily avoid the direction of the cue source. Dix & Hamilton hypothesize that since marsh periwinkles crawl up plant stems and leave the water when predator odours are present, snails increase their speed in an attempt to quickly locate the nearest stem. Similarly, Phillips (1975a,b) found that limpets (*Acmaea limatula* and *Acmaea scutum*) on a vertical surface move upward (negatively geotactic). When scent of predatory *Pisaster* flows over them from above they continue to move up the substratum but at an increased rate. Even though limpets do not change direction and avoid the predator cues, Phillips hypothesizes that the response is adaptive. He points out that *Acmaea* are generally higher than *Pisaster* in the intertidal zone; thus, a move upward would typically be a move to avoid the predator. In addition,

TABLE II. Behavioral responses to predator odor

Prey	Predator	Response	Author
KINGDOM PROTISTA			
Ciliate *Lambornella clarki*	Mosquito larvae *Aedes sierrensis*	Induced trophic shift	Washburn *et al.*(1988)
KINGDOM ANIMALIA			
Phylum Cnidaria			
Anemone *Anthopleura elegantissima*	Nudibranch *Aeolidia papillosa*	Alarm response (withdrawal)	Howe & Harris (1978)
Anemone *Stomphia coccinea*	Starfish *Dermasterias*	Escape (swimming)	Yentsch & Pierce (1955)
Phylum Mollusca			
CLASS GASTROPODA			
Gastropods	Starfish	Escape	Bullock (1953)
Various gastropods	Sea stars	Avoidance and escape	Feder (1967)
Ancylus fluviatilis	Stonefly, *Dinocras cephalotes*	Reduced activity	Malmqvist (1992),
Buccinum undatum	Sea star, *Marthasterias glacialis*	Shell twisting, escape	Feder & Arvidsson (1967)
B. undatum	Sea star and extracts (saponin)	Avoidance or convulsions	Mackie, Lasker & Grant (1968)
B. undatum	Sea star, *Leptasterias polaris*	Escape	Legault & Himmelman (1993)
Cittarium pica	Gastropod, *Thais spp.*	Escape (leave water)	Hoffman & Weldon (1978)
Fasciolaria tulipa	Larger conspecifics	Escape	Snyder & Snyder (1971)
Helisoma antrosum and *Pomacea paludosa*	Turtles	Burial	Snyder (1967)
Periwinkles, *Littorina scutulata*	Starfish	Escape	Feder (1963)
Littorina planaxis	Snail, *Acanthina spirata*	Escape	Peters (1964)
Littorina cincta & *L. unifasciata*	Whelk, *Lepsiella scobina*	Escape (climbing from tidepools)	McKillup (1981)
Marsh periwinkle *Littoraria irrorata*	Mucus from predatory neogastropods, esp. crown-conch, *Melongena corona*	Escape response	Dix & Hamilton (1993)
L. irrorata	Blue crab, *Callinectes sapidus*, turban snails, *Fasciolaria spp.* and crown conch, *M. corona*	Avoidance and escape	Duval, Calzetta & Rittschof, (1994)
Nassarius luteostoma	Gastropod, *Natica unifasciata*	Escape	Gonor (1964)
Nassarius vibex	Starfish, *Luidia alternata* & gastropod, *Fasciolaria hunteria*	Avoidance	Gore (1966)
Atlantic dogwhelk *Nucella lapillus*	Crab, *Cancer pagurus*	Decreased growth (dec. feeding?)	Palmer (1990)
N. lapillus	Crab, *Carcinus maenas*	Decreased feeding	Vadas, Burrows & Hughes (1994)
N. lamellosa	Crab, *Cancer productus*	Avoidance	Marko & Palmer (1991)
Olivella biplicata	Starfish, *Oronectes virilis*	Avoidance (burial)	Phillips (1977)
Whelk, *Buccinum undatum*	Seastar, *Leptasterias polaris*	Escape	Harvey, Gameau & Himmelman (1987)
Freshwater snail, *Physella virgata*	Crayfish, *Procambrus simulans*	Escape (climbing)	Alexander & Covich (1991)
Planaxis sulcatus	Gastropod, *Morula anaxeres*	Leave water	McKillup & McKillup (1993)
Various freshwater gastropods	Crayfish	Escape (climbing)	Covich *et al.* (1994)
Strombids	Prosobranchs, *Aulicia vespertilio* & *Conus marmoreus*	Escape (leaping)	Gonor (1966)
Strombus maculatus	Cone snails	Escape	Berg (1972; 1974)
S. maculatus	*Conus spp.* & *Cymatium spp.*	Escape	Field (1977)
Strombus raninus	*Fasciolaria tulipa*	Escape (leaping)	Snyder & Snyder (1971)
Black turban snail *Tegula funebralis*	Starfish	Escape	Feder (1963); Yarnall (1964); Burke (1964); Phillips (1978)
T. funebralis	Starfish *Pisaster ochraceus*	Escape (crawl out of water)	Szal (1971)
T. funebralis	Crab, *Cancer antennarius*	Avoidance	Geller (1982)
Thais emarginata	*Cancer productus*	Immobility, avoidance	Gosselin (1990)
Limpets *Acmaea spp.*	Starfish	Escape	Feder (1972); Phillips (1975a,b; 1976)
Keyhole limpet, *Diodora aspera*	Starfish	Mantle response	Margolin (1964)

(continued on next page)

TABLE II. (continued)

Prey	Predator	Response	Author
Limpets, *Siphonaria sirius* & *Cellana toreuma*	Whelk, *Thais clavigera* Starfish, *Coscinasterias acutispina*	Escape Escape (*Cellana* only)	Iwasaki (1993)
Abalone *Haliotis spp.*	Starfish *Pycnopodia helianthoides* & *Pisaster ochraceus*	Escape	Montgomery (1967)
CLASS BIVALVIA			
Scallops *Pecten maximus* & *Chlamys opercularis*	Gastropod *Buccinum undatum*	Escape	Mackie & Grant (1974)
P. maximus	Starfish, *Asterias glacialis*	Escape	Fange (1963)
Phylum Arthropoda			
CLASS CRUSTACEA			
Daphnia	*Chaoborus, Notonecta* & bluegill sunfish, *Lepomis macrochirus*	Avoidance	Dodson (1988b)
Daphnia galeata × *hyalina*	Bleak, *Leucaspius delineatus*	Diel vertical migration	Loose (1993a,b)
D. galeata mendotae	Bluegill sunfish, *Lepomis macrochirus*	Move to deeper water	Stirling (1995)
Daphnia hyalina	Perch, *Perca fluviatilis*	Increased diel migration	Ringelberg (1991a,b,c)
Daphnia longispina	*Notonecta*	Reduced polarotaxis	Watt & Young (1994)
Daphnia magna	Fish, *Leucaspius delineatus*	Diel vertical migration	Dawidowicz & Loose (1992)
D. magna	Roach, *R. rutilus*	Increased neg. phototaxis	DeMeester (1993)
D. magna	Various fish	Increased neg. phototaxis	Loose, Von Ellert & Dawidowicz (1993)
D. magna	Fish, *Leusaspius delineatus*	Increased vertical migration	Loose & Dawidowicz (1994)
D. magna	Goldfish, *Carassius auratus*	Inc. vertical migration (upward)	Watt & Young (1994)
D. magna	green sunfish, *Lepomis cyanellus*	Avoidance	Lauridsen & Dadge (1996)
Daphnia pulex	*Chaoborus americanus*	Upward movement	Ramcharan, Dodson & Lee (1992)
D. pulex	*Chaoborus*	Avoidance	Kvam (1993)
D. pulex, D. longispina	*Chaoborus flavicans*	Avoidance	Kvam & Kleiven (1995)
Copepod, *Diaptomus kenai*	*Chaoborus trivittatus*	Induced vertical migration	Neill (1990)
Copepod, *Diaptomus tyrrelli*	Copepod, *Epischura nevadensis*	Reduced filtering, avoidance	Folt & Goldman (1981)
Isopod, *Asellus aquaticus*	Amphipod, *Gammarus pulex*	Increased respiration, exudation of amino acids	Bengtsson (1982)
Isopod, *Lirceus fontinalis*	Green sunfish, *Lepomis cyanellus*	Decreased activity	Holomuzki & Short (1988; 1990)
L. fontinalis	Various fish	Reduced movement	Short & Holomuzki (1992)
Amphipod, *Gammarus minus*	Green sunfish, *Lepomis cyanellus*	Decreased activity	Holomuzki & Hoyle (1990)
Amphipod, *Gammarus pseudolimnaeus*	Various fish	Decreased activity	Williams & Moore (1982; 1985)
Amphipod, *Gammarus pulex*	Sculpin, *Cottus gobio*	Decreased activity	Andersson *et al.* (1986)
G. pulex	Brown trout, *Salmo trutta*	Reduced night drift of large indiv.	Friberg *et al.* (1994)
Ostracod, *Cypridopsis vidua*	Bream, *Abramis brama*	Decreased motility	Roca & Danielopol (1996)
C. vidua	*A. brama*	Altered habitat use and inc. swimming	Uiblein *et al.* (1996)
C. vidua	*A. brama*	Increased use of vegetation	Roca, Boltanas & Uiblein (1993)
C. vidua	*A. brama*	Altered swimming paths	Uiblein, Roca & Danielopol (1994)
Barnacle, *Balanus glandula*	Whelk, *Nucella lamellosa*	Decreased larval settlement	Johnson & Strathmann (1989)
Antarctic krill, *Euphausia superba*	Vertebrate nitrogenous waste	School dispersion, sinking	Strand & Hamner (1990)
American lobster, *Homarus americanus*	Sculpin	Increased shelter use	Wahle (1989)
H. americanus (postlarvae)	Cunner, *Tautogolabrus adspersus*	Avoidance in maze Less selective settlement behaviour	Boudreau, Bourget & Simard (1993b) Boudreau, Bourget & Simard (1993a)
H. americanus	Sculpin *Myoxocephalus anaeus*	Increased shelter use	Wahle (1992)
Signal crayfish, *Pacifastacus leniusculus*	Perch, *Perca fluviatilis*; eel, *A. anguilla*	Reduced activity; inc. shelter use	Blake & Hart (1993)
Crayfish, *Paranephrops zelandicus*	Eel, *Anguilla dieffenbachii*	Defensive posture	Shave, Townsend & Crowl (1994)
Crayfish, *Oronectes rusticus*	Largemouth bass, *Micropterus salmoides*	Increased shelter use	Willman, Hill & Lodge (1994)

(continued on next page)

TABLE II. (continued)

Prey	Predator	Response	Author
Stream invertebrates (including insects)	Rainbow trout, *Oncorhynchus mykiss*	Increased drift	Williams (1990)
Freshwater shrimp, *Atya lanipes*	*Macrobrachium carcinus*	Avoidance; altered habitat use	Crowl & Covich (1994)
Brine shrimp, *Artemia spp.*	Atlantic menhaden, *Brevoortia tyrannus*	Downward movt. with inc. light	Forward & Rittschof (1993)
Brine shrimp, *A. franciscana*	Menhaden, mummichog, pinfish ctenophores (*Mnemiopsis leidyi*)	Neg. phototaxis with inc. light	McKelvey & Forward (1995)
Hermit crab, *Clibanarius vittatus*	Stone crab, *Minippe mercenaria*	Increased in locomotion	Hazlett (1996)
CLASS INSECTA			
Mayflies (4 *spp.*)	Stoneflies (4 *spp.*)	Reduced settlement	Peckarsky (1980); Peckarsky & Dodson (1980)
Mayfly, *Baetis bicaudatus*	Trout	Avoidance	Cowans & Peckarsky (1994)
B. bicaudatus	Brook trout, *Salvelinus fontinalis*	Reduced night-time drift	McIntosh & Peckarsky (1996)
B. tricaudatus	Mottled sculpin, *Cottus bairdi*	Reduced foraging; inc. downstream drift	Kohler & McPeek (1989)
Mayfly, *B. coelestis*	Rainbow trout, *O. mykiss*	Reduced daytime drift	Douglas, Forrester & Cooper (1994)
B. rhodani & *B. subalpinus*	Minnow, *Phoxinus phoxinus*	Reduced daytime drift	Tikkanen, Muotka & Huhta (1994)
Mayflies	Stoneflies; fish	Avoidance	Martinez (1987); Martinez & Peckarsky (1993)
Mayflies, *Ephemerella aurivilli* & *Paraleptophlebia heteronea*	Dace, *Rhinichthys cataractae*	Avoidance	Scrimgeour, Culp & Cash (1994)
Mayfly nymph, *Paraleptophlebia adoptiva*	Stonefly nymph, *Acroneuria carolinensis*	Increased sensitivity to contact with stonefly	Ode & Wissinger (1993)
Caddisflies, *Silo pallipes*, *Agapetus ochripes*; Mayfly, *Baetis rhodani*	Stonefly, *Dinocras cephalotes*	Avoidance (*S. p.*); Reduced activity (*A. o.* & *B. r.*)	Malmqvist (1992)
Caddisfly, *Agapetus ochripes*	Sculpin, *Cottus gobio*	Reduced activity	Malmqvist (1992)
Stoneflies, *Paragnetina media* *Phasganophora capitata*	Rainbow trout *Oncorhynchus mykiss*	Altered activity (increase in *P. media*; dec. in *P. capitata*)	Williams (1986)
Stoneflies	Fish	Avoidance	Martinez (1987); Martinez & Peckarsky (1993)
Damselfly, *Ischnura elegans*	*Notonecta glauca*	Decreased feeding rate	Heads (1986)
Mosquito, *Culex pipiens* (larvae)	*Notonecta undulata*	Decreased movement	Sih (1986)
Mosquito, *Anopheles punctipennis*, & phantom midge *Chaoborus albatus* (larvae)	Bluegill sunfish, *Lepomis macrochirus* & green frog, *Rana clamitans* (*A.p.* only)	Avoidance of egg-laying sites	Petranka & Fakhoury (1991)
Chaoborus flavicans (larvae)	Three-spined stickleback, *Gasterosteus aculeatus*	Vertical migration; increase depth in water column	Dawidowicz, Pijanowska & Ciechomski (1990); Dawidowicz (1993)
Chaoborus spp. (larvae)	Fish (minnows and sunfish)	Increase vertical migration	Tjossem (1990)
Chironomus tentans (larvae)	Pumpkinseed sunfish, *Lepomis gibbosus*	Red. activity (inc. time hiding)	Macchiusi & Baker (1992)
Phylum Echinodermata			
Starfish, *Asterias rubens*	Starfish, *Solaster papposus*	Avoidance	Castilla & Crisp (1970)
Ophiuroid, *Ophiothrix fragilis*	Starfish, *Marthasterias glacialis*	Escape	Feder & Arvidsson (1967)
Sea urchin *Strongylocentrotus droebachiensis*	Lobster, *Homarus americanus* & crab, *Cancer irroratus*	Avoidance	Mann *et al.* (1984)
S. droebachiensis	Lobster, rock crabs, *Cancer spp.* & cunner, *Tautogolabrus adspersus*	Avoidance	Scheibling & Hamm (1991)
Sea urchin *Strongylocentrotus purpuratus*	Sea star *Pycnopodia helianthoides*	*Pedicellaria* response	Phillips (1978)
Sand dollars	Starfish, *Pisaster brevispinus*	Burial	MacGinitie & MacGinitie (1968)
Holothurian, *Cucumaria frondosa*	Sea star, *Solaster endeca*	Escape	Legault & Himmelman (1993)
Phylum Chordata, Subphylum Vertebrata			
CLASS OSTEICHTHYES			
Brook trout *Salvelinus fontinalis* (juveniles)	Pickerel, *Esox americanus* and Atlantic salmon, *Salmo salar*	Avoidance	Keefe, Whitesel & Winn (1991)
S. fontinalis	Redfin pickerel, *Esox americanus*; Atlantic salmon *Salmo salar* (if piscivorous)	Avoidance	Keefe (1992)

(continued on next page)

TABLE II. (continued)

Prey	Predator	Response	Author
Pacific salmon, *Oncorhynchus spp.*	Mammals (skin rinse)	Cessation of upstream movement; alarm reaction	Idler, Fagerlund & Mayoh (1956); Brett & MacKinnon (1952; 1954); Alderdice *et al.* (1954)
Coho salmon *Oncorhynchus kisutch* (juveniles)	Squawfish *Ptychocheilus oregonensis*	Avoidance, inc. plasma cortisol and glucose	Rehnberg & Schreck (1987)
O. kisutch (juveniles)	Amino acids from mammal skin	Avoidance	Rehnberg, Jonasson & Schreck (1985)
O. kisutch (juveniles)	Common merganser, *Mergus merganser*	Decreased activity, including foraging and aggression	Martel (1996); Martel & Dill (1993)
Starry goby *Asterropteryx semipunctatus*	Lizardfish *Synodus variegatus*	Decreased movement, increased bobbing	Smith (1989)
Cyprinid fishes	Predatory fish species	Alarm reaction	Reed (1969)
Cyprinid fishes	Fish	Defensive behavior	Malyushina, Kasumyan & Marvsov (1991)
Goldfish, *Carassius auratus*	Bullhead, *Ictalurus melas*	Avoidance (inconsistent)	Davy & Kleerekoper (1971)
European minnow, *Phoxinus phoxinus*	Pike, *Esox lucius*	Flight	von Frisch (1941a,b)
P. phoxinus	Pike	Escape or inhibition of behaviour	Goz (1941)
P. phoxinus	Pike, *Esox lucius*	Hiding and schooling	Magurran (1989)
Fathead minnow, *Pimephales promelas*	Pike, *Esox lucius*	Reduced activity; increased refuge use;	Mathis & Smith (1993a,b); Chivers & Smith (1993; 1994); Mathis, Chivers & Smith (1993); Brown, Chivers & Smith (1995a)
P. pimephales	*E. lucius*	Greater shoal cohesion when familiar individuals together	Chivers, Brown & Smith (1995b)
P. pimephales	*E. lucius*	Reduced foraging after acquired recognition	Brown & Smith (1996)
P. pimephales	Garter snake *Thamnophis radix* and *T. sirtalis*	Sympatric males freeze and increased shelter use; females do not respond	Matity, Chivers & Smith (1994)
P. pimephales	*E. lucius* (faeces)	Avoidance	Brown, Chivers & Smith (1995)
Bitterling, *Rhodeus sericesu*	Pike, *Esox lucius*	Avoidance	Kasumyan & Pashchenko (1985)
Paradise fish, *Macropodus opercularis*	Snakehead, *Channa micropeltes*	Increased activity	Gerlai (1993)
Mosquitofish, *Gambusia patruelis*	Pickerel, *Esox americanus*	Escape swimming	George (1960)
Cichlid, *Oreochromis mozambicus*	Snakehead, *Channa striatus*	Avoidance	Jaiswal & Waghray (1990)
Damselfish, *Stegastes partitus*	Brittlestar, *Ophiocoma echinata*	Avoidance of nest sites	Knapp (1993)
Brook stickleback, *Culaea inconstans*	Northern pike, *Esox lucius*	Decreased activity	Gelowitz *et al.* (1993)
C. inconstans	*E. lucius*	Inccreased schooling, movement toward substrate	Chivers, Brown & Smith (1995a)
Bleak, *Alburnus alburnus*	*E. lucius*	Hiding or shoaling	Jachner (1995a)
A. alburnus	*E. lucius*	Reduced feeding	Jachner (1995b)
CLASS AMPHIBIA			
Various amphibian larvae	*Lepomis cyanellus*	Increased refuge use	Kats, Petranka & Sih (1988)
Small-mouthed salamander, *Ambystoma barbouri*	*Lepomis cyanellus*	Freezing (no refuges) or hiding	Sih & Kats (1991; 1994)
A. barbouri	Green sunfish, *Lepomis cyanellus*	Increased refuge use (day) & nocturnal drift	Sih, Kats & Moore (1992)
Ambystoma talpoideum (tadpoles)	Bluegill sunfish, *Lepomis macrochirus*	Increased refuge use	Jackson & Semlitsch (1993)
Small-mouthed salamander, *Ambystoma texanum* (larvae)	Green sunfish, *Lepomis cyanellus*	Increased refuge use	Kats (1988)
Salamander, *Desmognathus monticola*	*Desmognathus quadramaculatus*	Avoidance	Roudebush & Taylor (1987)
Salamanders, *Plethodon spp*	Ringneck snake, *Diadophis punctatus*	Avoidance	Cupp (1994)
California newt, *Taricha torosa* (hatchlings)	Conspecific adults	Increased time in refuge	Kats *et al.* (1994); Elliott, Kats & Breeding (1993)
Tailed frog *Ascaphus truei* (tadpoles)	Salamanders, *Dicamptodon copei*; trout, *Salmo clarkii* & *Salvelinus fontinalis*	Reduced feeding activity	Feminella & Hawkins (1992; 1994)
Treefrog, *Hyla versicolor* & salamander, *Eurycea bislineata* (larvae)	*Lepomis cyanellus*	Increased refuge use; avoidance	Petranka, Kats & Sih (1987)
Treeforg, *Hyla chrysoscelis* (tadpoles)	*Lepomis macrochirus*, crayfish *Procambarus clarki*	Induced refuge use	Bridges & Gutze (1997)
Red-legged frog, *Rana aurora* (tadpoles)	Newt, *Taricha granulosa*	Reduced movement	Wilson & Lefcort (1993)
Rana lessonae & *R. esculenta* (tadpoles)	Pike, *Esox lucius*	Decreased swimming	Stauffer & Semlitsch (1993)
Pickerel frog, *Rana palustris* & American toad, *Bufo americanus* (tadpoles)	Longear sunfish, *Lepomis megalotis*	Reduced activity	Holomuzki (1995)

(continued on next page)

TABLE II. (continued)

Prey	Predator	Response	Author
Bullfrog, *Rana catesbeiana* tadpoles	Salamander, *Taricha granulosa*	Reduced movement	Lefcort & Eiger (1993)
Southern leopard frog, *Rana utricularia* (tadpoles)	Siren, *Siren intermedia*, Warmouth sunfish, *Lepomis gulosus*	Reduced movement	Lefcort (1996)
European frog, Rana temporaria (tadpoles)	Fish, *Perca fluviatilus, Rutilus rutilus* and *Percottus glehni*	Avoidance	Manteifel (1995)
Western toad (*Bufo boreas*) tadpoles	Backswimmer; *Notonecta spp.*, giant waterbug, *Lethocerus americanus* garter snake, *Thamnophis sirtalis*	Reduced movement and increased refuge use	Kiesecher, Chivers & Blaustein (1996)
CLASS REPTILIA			
Broad-headed skink, *Eumeces laticeps*	Snake, *Lampropeltis*	Increased tongue flicking	Cooper (1990)
Banded gecko, *Coleonyx variegatus*	Snake, *Phyllorhynchus decurtatus*	Tail display	Dial (1990); Dial, Weldon & Curtis (1989)
Common lizard, *Lacerta vivipara*	Predatory snakes: viper, *Vipera berus* smooth snake, *Coronella austriaca*	Inc. tongue flicking, slow movement	Thoen, Bauwens & Verheyen (1986)
L. vivipara	*Vipera berus*	Increased tongue flicking, decreased movement	VanDamme *et al.* (1990)
Monitor lizard, *Varanus albigularis*	Horned adder, *Bitis caudalis*; spitting cobra, *Naja nigricollis*	Defense/aggressive behaviors	Phillips & Alberts (1992)
Lizard, *Podarcis hispanica*	Viper, *Vipera latastei*	Dec. movement, inc. tongue flicking	VanDamme & Castilla (1996)
New world pit vipers (Crotalines)	Colubrid snakes	Body bridging	Weldon & Burghardt (1979)
Crotaline snakes	Ophiophagous snakes	Defensive reaction	Marchisin (1980)
Various crotalines	Kingsnake, *Lampropeltis getulus*	Defensive responses, including body bridging	Gutzke, Tucker & Mason (1993)
Rattlesnakes, *Crotalus spp.*	Kingsnake, *Lampropeltis getulus* Spotted skunk, *Spilogale phenax*	Heart rate increase Body loop & strike	Cowles & Phelan (1958); Cowles (1938)
Side-winder, *Crotalus cerastes*	Kingsnake, *Lampropeltis getulus*	Body loop (defense posture)	Bogert (1941)
Prairie rattle-snake, *Crotalus viridis* & water moccasin, *Agkistrodon piscivorus*	Kingsnake, *Lampropeltis getulus*	Reduced exploratory behaviour	Chizar *et al.* (1978)
Pinesnake, *Pituophis melanoleucus*	Kingsnakes and milksnakes *Lampropeltis spp.*	Avoidance, tongue flicking	Burger (1989; 1990)
P. melanoleucus	Kingsnake, *Lampropeltis getulus*	Avoidance	Burger *et al.* (1991)
Corn snake, *Elaphe guttata*	Kingsnake, *Lampropeltis getulus*	Increased tongue flicking	Weldon, Ford & Perry-Richardson (1990)
Garter snakes *Thamnophis spp.*	Kingsnake, *L. getulus* & black racer, *Coluber constrictor*	Increased tongue flicking	Weldon (1982)
Muskturtle *Sternotherus*	Alligator snapping turtle, *Macroclemys temmincki*	Avoidance, slows down	Jackson (1990)
CLASS AVES			
European starling, *Sturnus vulgaris*	Component of mustelid scent glands (ortho-aminoacetophenone)	Avoidance of contaminated food	Mason, Clark & Shaw (1991)
CLASS MAMMALIA			
Swamp wallaby, *Wallabia bicolor*	Dog urine	Avoidance of treated food plants	Montague, Pollock & Wright (1990)
Tenrecs	Viverrids	Defensive reaction	Eisenberg & Gould (1970)
California ground squirrel, *Spermophilus beecheyi*	Rattlesnake, *Crotalus viridis* & gopher snake, *Pituophis melanoleucus*	Approach and harassment	Hennessy & Owings (1978)
House mouse, *Mus musculus*	Rat snake, *Elaphe obsoleta*	Inc. defecation, dec. feeding on tainted food	Weldon, Divita & Middendorf (1987)
M. musculus	Synthetic stoat (*Mustela erminea*) anal gland secretion & fox (*Vulpes vulpes*) fecal component	Avoidance of tainted food	Coulston, Stoddar & Crump (1993)
M. musculus	Cat, *Felis domesticus*; shrew, *Blarina brevicauda*	Avoidance	Drickamer *et al.* (1992)
Mouse, *Mus musculus domesticus*	Red fox, *V. vulpes*; cat, *Felis catus;* Western quoll, *Dasyurus geoffroii*	Avoidance of tainted traps; Inc. use of vegetated habitats	Dickman (1992)
M. musculus domesticus	Cat	Analgesic response	Kaveliers & Colwell (1996)

(continued on next page)

TABLE II. (continued)

Prey	Predator	Response	Author
Rattus and *Mus*	Marten urine	Avoidance	Reiff (1956)
White rat	Cat	Freeze and huddle	Griffith (1920)
Rat	Cat	Suppression of approach to water	Courtney *et al.* (1968)
Rat	Skunk odor (artificial)	Avoidance	Ford & Clausen (1941)
Rat	Cat	Cautious behavior	Blanchard *et al.* (1990)
Rat	Cat	Females inc. defensive behaviors and ultrasonic vocalizations	Blanchard *et al.* (1991)
Rat	Cat	Less time in social interactions	Zangrosi & File (1992)
Rat	Weasel, *Mustela erminea*	Avoidance of contaminated food	Heale & Vanderwolf (1994)
Rat, *Rattus norvegicus*	Fox, *Vulpes vulpes* feces	Freezing, hiding, inc. excretion, physiological arousal, inc. sniffing, inc. vigilance, inhib. of learned behavior inhib. of vocalization	Cattarelli (1982 a,b); Cattarelli & Chanel (1979); Cattarelli & Vigouroux (1981); Cattarelli *et al.* (1974; 1977a,b); Vernet-Maury (1970; 1980); Vernet-Maury *et al.* (1982; 1984; 1991)
R. norvegicus	Cat	Reduced foraging	Whishaw & Dringenberg (1991)
Apodemus sylvaticus (males only)	Red fox, *Vulpes vulpes*	Avoidance	Dickman & Doncaster (1984)
A. sylvaticus & *Clethrionomys glareolus*	Mink, *Mustela vison*	Avoidance	Robinson (1990)
Bank vole, *Clethrionomys glareolus*	Weasel, *Mustela nivalis*	Avoidance	Jedrzejewski & Jedrzejewska (1990)
C. glareolus	Mustelids (4 *spp.*) & canids (2 *spp.*)	Avoidance and dec. activity (to weasel and red fox)	Jedrzejewski, Rychlik & Jedrzejewska (1993)
C. glareolus (females)	Stoat, *Mustela erminea*	Decreased activity, avoidance of males	Ylönen & Ronkainen (1994); Ronkainen & Ylönen (1994)
Voles, *Microtus*	Stoat, *Mustela erminea* & red fox, *Vulpes vulpes*	Avoidance	Sullivan, Crump & Sullivan (1988a)
Microtus	Stoat, *Mustela erminea*	Avoidance	Gorman (1984)
Short-tailed vole, *Microtus agrestis*	Tiger, *Panthera tigris* urine	Avoidance (reduced trap catches)	Stoddart (1982)
M. agrestis	Weasel, *Mustela nivalis*	Avoidance	Stoddart (1976; 1980)
M. agrestis	Mink, *Mustela vison* Least weasel, *M. n. nivalis*	Decreased foraging and mating	Koskela & Ylönen (1995)
Microtus arvalis	Red fox, *V. vulpes* (faeces)	Avoidance	Calder & Gorman (1991)
Montane vole, *Microtus montanus*	Short-tailed weasel, *Mustela erminea*	Reduced feeding	Sullivan, Crump & Sullivan (1988a); Sullivan *et al.* (1988)
M. montanus	*Mustela erminea*	Avoidance	Sullivan *et al.* (1990b)
Meadow vole, *Microtus pennsylvanicus*	Short-tailed shrew, *Blarina brevicauda*	Avoidance	Fulk (1972)
M. pennsylvanicus	Short-tailed weasel, *Mustela erminea*	Avoidance	Parsons & Bondrup-Neilsen (1996)
M. pennsylvanicus	red fox, *V. vulpes* (synthetic odour)	males reduced movement females no effect	Perrot-Sinal *et al.* (1996)
Townsend's vole, *Microtus townsendii*	Synthetic mustelid odor	Avoidance	Merkens, Harestad & Sullivan (1991)
White-footed mouse, *Peromyscus leucopus*	Short-tailed weasel, *Mustela erminea*	Analgesia	Kavaliers (1988)
Deer mouse, *Peromyscus maniculatus*	Short-tailed weasel, *Mustela erminea*	Inc. latency of response to aversive stimuli (analgesia)	Kavaliers (1990) Kavaliers, Innes & Ossenkopp (1991)
Syrian hamster, *Mesocricetus auratus*	Dog, cat, polecat	Threat, attack, freeze, escape	Dieterlen (1959)
Kangaroo rat, *Dipodomys merriami*	Sidewinder rattlesnake, *Crotalus cerastes*	Avoidance	Webster (1973)
Kangaroo rats, *Dipodomys deserti* & *D. merriami*	Sidewinder, *Crotalus cerastes*	Decreased feeding	Bouskila (1993)
D. spectabilis	Mojave rattlesnake, *Crotalus scutulatus* Gopher snake, *Pituophis melanoleucus*	Approach and inspect	Randall, Hatch & Hekkala (1995)
Wood rat, *Neotoma albigula*	Garter snake	Alarm (foot thumping)	Richardson (1942)
Northern pocket gopher, *Thomomys talpoides*	*Mustela spp.*	Avoidance (inconsistent)	Sullivan & Crump (1986a); Sullivan, Crump & Sullivan (1988b) Sullivan, *et al.* (1990a)
Mountain beaver, *Aplodontia rufa*	Mink gland secretion, carnivore urine (mink, bobcat, coyote, dog)	Avoidance of food dishes	Epple *et al.* (1993)
A. rufa	?	Avoidance	Nolte *et al.* (1993)
A. rufa	Urine (mink, coyote)	Avoidance of contaminated food	Mason, Epple & Nolte (1994)

(continued on next page)

TABLE II. (concluded)

Prey	Predator	Response	Author
A. rufa	Urine (coyote), synthetic mustelid gland secretions	Avoidance of contaminated food	Epple *et al.* (1995)
A. rufa, Mus musculus, Peromyscus maniculatus and guinea pigs, *Cavia porcellus*	Coyote, *Canis latrans* (urine)	Avoidance of food dishes	Nolte *et al.* (1994)
Beaver, *Castor canadensis*	Fecal extracts (wolf, coyote, dog black otter, lynx, African lion)	Avoidance of contaminated food	Engelhart & Müller-Schwarze (1995)
Woodchuck, *Marmota monax*	Bobcat urine	Avoidance	Swihart (1991)
Porcupine *Erethizon dorsatum*	Bobcat & coyote urine	Increased breathing rate & vigilance; escape (running)	Sweitzer & Berger (1992)
Snowshoe hare, *Lepus americanus*	Mustelid anal gland secretions, carnivore urine	Avoidance	Sullivan & Crump (1984, 1986b); Sullivan, Nordstrom & Sullivan (1985a)
L. americanus	Wolverine, *Gulo gulo* urine	Reduced feeding	Sullivan (1986)
Rabbit, *Oryctolagus cuniculus*	Mink, *Mustela vison*	Avoidance	Robinson (1990)
O. cuniculus	Synthetic lion feces	Avoidance	Boag & Mlotkiewicz (1994)
Alpine goat, *Capra hircus*	Various carnivores (and gazelles)	Avoidance of contaminated food	Weldon, Graham & Mears (1993)
Red deer, *Cervus elaphus*	Lion feces	Avoidance	Abbott *et al.* (1990)
Red deer, *C. elaphus* & Roe deer, *Capreolus capreolus*	Lion feces	Suppression of feeding	Vanhaaften (1963)
White-tailed deer, *Odocoileus virginianus*	Wolf scats	Avoidance	Müller-Schwarze (1983)
O. virginianus	Bobcat, *Lynx rufus* & coyote, *Canis latrans* urine	Avoidance	Swihart, Pignatello & Mattina(1991)
Black-tailed deer, *Odocoileus hemionus*	Coyote, mountain lion, lion, tiger, snow leopard	Avoidance	Müller-Schwarze (1972)
Mule deer, *Odocoileus hemionus*	Coyote, *Canis latrans* urine	Avoidance of tainted food pellets	Andelt, Burnham & Manning (1991)
Black-tailed deer, *O. hemionus columbianus*	Mammalian carnivore urine or feces	Avoidance, feeding suppression	Sullivan, Nordstrom & Sullivan (1985b); Melchiors & Leslie (1985)
Elk (female) *Cervus elaphus nelsoni*	Coyote, *Canis latrans* urine	Avoidance of contaminated food	Andelt, Baker & Burnham (1992)
Wapiti, *Cervus elaphus canadensis*	Mustelid gland secretions; dog wolf coyote, cougar faeces; dog, fox urine	Heart rate increased	Chabot, gagnon & Dixon (1996)
Cape grysbok, *Raphicerus milanotis* & duiker, *Sylvicapra grimmia*	Leopard, *Panthera pardus*; caracal, Felis caracal urine	Increased sniffing	Novellie, Bigalke & Pepler (1982)
Prey (various)	Lion, *Panthera leo*	Avoidance	Schaller (1972)
Domestic sheep, *Ovis aries*	Dog, *Canis familiaris* & lion, *Panthera leo* feces	Avoidance of contaminated food	Arnould & Signoret (1993)
Sheep, *O. aries* & cattle, *Bos taurus*	Coyote, fox, cougar fecal odor	Avoidance of contaminated feed	Pfister, Müller-Schwarze & Balph (1990)
Red-belly tamarin, *Saguinus labiatus*	Jaguar, margay, and jaguarundi feces	Avoidance & alarm calls	Caine & Weldon (1989)

he proposes that the currents in wave-swept intertidal areas probably do not provide consistent information about the location of cue sources.

Escape or avoidance behaviours have also been noted for bivalves (Fange, 1963; Mackie & Grant, 1974), crustaceans (Folt & Goldman, 1981) and echinoderms (Feder & Arvidsson, 1967; Castilla & Crisp, 1970; Mann *et al.*, 1984; Scheibling & Hamm, 1991; also see review by Mackie, 1974). MacGinitie & MacGinitie (1968) noted that sand dollars show increased burying in response to odours of predatory sea stars.

Early work on chemosensory-mediated predator-prey interactions of vertebrates was carried out on fish (von Frisch, 1941a,b; Goz, 1941). von Frisch noted frenetic escape swimming behaviours of European minnows (*Phoxinus phoxinus*) in response to pike (*Esox sp.*) chemical cues; however, he suspected that the response was a conditioned response rather than a naive response to predator cues. Magurran (1989) confirmed the importance of conditioning in these prey. In her study, European minnows did not respond initially to odours of pike, but did acquire responses to odours of both predatory pike and non-predatory tilapia (*Tilapia mariae*) when they were presented in conjunction with a potentially dangerous situation (*e.g.*, the presence of Schreckstoff). George (1960) found that mosquito fish (*Gambusia patruelis*) exhibit escape behaviours in response to pike odours without previous exposure to the odours, and Kasumyan & Pashchenko (1985) noted that bitterling (*Rhodeus sericesu*) also avoid pike chemical cues.

Coho salmon juveniles (*Oncorhynchus kisutch*) stay away both from chemical cues from predatory squawfish (*Ptychocheilus oregonensis*) (Rehnberg & Schreck, 1987) and from water-borne amino acids originating from mammalian skin (Rehnberg, Jonasson & Schreck, 1985). Brett & MacKinnon (1952; 1954) and Alderdice *et al.* (1954) found that Pacific salmon (*Oncorhynchus sp.*) cease moving upstream in response to mammalian skin rinses. Idler, Fagerlund & Mayoh (1956) noted that l-serine causes fish to stop moving up a fish ladder, while other amino acids do not cause cessation of movement.

However, not all fish studies found chemical sensitivity to predators. In a very thorough study, Barnett (1982) used a y-maze to investigate chemical cue responses of captive born naive cichlid (*Cichlasoma citrinellum*) fry to chemical cues from conspecifics and predatory heterospecifics. Fry preferred conspecific cues over control cues and also preferred cues of their mother over cues from other cichlid fry. Fry showed no avoidance, however, of cues from two predatory congeners (*C. managuense, C. nigrofasciatum*).

While there are many studies that have examined the effect of predator chemical cues on amphibians and reptiles, only a few have noted conspicuous avoidance behaviour on the part of the prey. Petranka, Kats & Sih (1987) noted that two-lined salamander (*Eurycea bislineata*) larvae avoid chemical cues from predatory green sunfish (*Lepomis cyanellus*). Two studies on adult plethodontid salamanders found that they are capable of detecting and avoiding odours from predatory congeners (Roudebush & Taylor, 1987) and snakes (Cupp, 1994). Pinesnakes (*Pituophis melanoleucus*) avoid cues from predatory kingsnakes (*Lampropeltis sp.*) (Burger, 1989; Burger *et al.*, 1991), and musk turtles (*Sternotherus odouratus*) avoid alligator snapping turtle (*Macroclemys temmincki*) odours (Jackson, 1990).

After the literature on gastropods, the next most extensive literature on chemically-mediated predator avoidance concerns mammals, due in large measure to the practical implications of such research. For example, Sullivan, Crump & Sullivan (1988a,b) used chemicals from stoat (*Mustela erminea*), ferrets (*Mustela putorius*), and red fox (*Vulpes vulpes*) to reduce the feeding damage of herbivorous pocket gophers (*Thomomys talpoides*) and voles (*Microtus spp.*) on agricultural crops. In laboratory studies, the gophers avoided a component of fox feces but did not avoid components of fox urine or chemical cues from ferrets or stoats. Further studies (Sullivan *et al.*, 1990a,b) used synthetic predator cues and tested the effectiveness of various devices for controlled-release of the chemicals. Voles (*Microtus pennsylvanicus*) decrease their use of nest boxes when the boxes contain shrew (*Blarina brevicauda*) droppings (Fulk, 1972). *Microtus agrestis* are captured significantly less often in traps that contain weasel (*Mustela nivalis*) chemical cues than in control traps; however, woodmice (*Apodemus sylvaticus*) are caught equally as often in experimental traps as they are in control traps (Stoddart, 1976). Weasel prey on both species of rodents. House mice avoid traps that contain cat or shrew feces, but are neutral towards traps that contain dog feces (Drickamer, Mikesic & Shaffer, 1992). One study addressed the long term role of predator odours on rodents (Sullivan *et al.*, 1988). They found that vole populations declined significantly in three consecutive winters in areas that were treated with predator odours. They concluded that the declines were a result of increased mortality of rodents caused by increased predation and possible physiological stress induced by predator odours. Higher numbers of predators may have resulted from them being attracted to study sites that contained predator odours.

Only one study has examined the responses of primates to predator chemical cues (Caine & Weldon, 1989). Red-bellied tamarins (*Saguinus labiatus*) were exposed to methylene chloride extracts of feces of the jaguar (*Pantera onca*), margay (*Felis wiedi*), jaguarundi (*Herpailurus yagouaroundi*), tapir (*Tapirus terrestris*), paca (*Cuniculus paca*), and agouti (*Dasyprocta fuliginosa*). Tamarins avoid the odours of the three potential predators (jaguar, margay and jaguarundi) more than odours of the nonpredatory species (tapir, paca and agouti). All tamarins were captive-born, indicating that they do not have to have experience with predators to recognize their odours.

The behavioural responses of prey discussed so far are relatively short-term responses to predator chemical cues that may or may not occur regularly, depending on the presence or absence of the predator. In some prey animals, escape or avoidance reactions in response to predators have taken on a regular daily pattern. Neill (1990) found that the freshwater copepod (*Diaptomus kenai*) has a normal daily pattern of descending to deep water (> 8 m) at night and ascending to shallow water (< 8 m) during the day, but that these vertical migrations cease when a predator (*Chaoborus trivittatus*) is absent. Vertical migration can be induced in copepods by simply adding water from a tank holding chaoborids, indicating that chemical cues are probably very important in mediating the behaviour. Similarly, vertical migration in chaoborids appears to be in response to fish chemical cues (Dawidowicz, Pijanowska & Ciechomski, 1990; Tjossem, 1990). *Chaoborus* larvae exposed either to caged fish (*Gasterosteus aculeatus*) or to water treated with fish spend significantly more time in bottom sediments during the day than do control larvae (Dawidowicz, Pijanowska & Ciechomski, 1990). Caged predatory fish (*Gasterosteus aculeatus*) do not induce diel vertical migrations in the marine copepod *Acartia hudsonica* (Bollens & Frost, 1989; Bollens, Frost & Cordell, 1994). However, these copepods migrate in response to free-swimming fish indicating they might be responding to physical or visual stimuli or to chemicals from injured/consumed conspecifics. Each of these daily responses is probably a result of selection on prey to limit activity to parts of the day when their predator is least active or to areas within the habitat where predators are least common.

Prey organisms that drift in aquatic habitats show adaptive responses when it comes to settling out of the current onto substrate that is a potentially risky site. Stream dwelling mayfly nymphs apparently use cues from predatory stoneflies to select benthic substrates on which to settle (Peckarsky, 1980; Peckarsky & Dodson, 1980). Mayflies, like many other aquatic invertebrates, move in streams via passive or active drift mechanisms. Peckarsky (1980) and Peckarsky & Dodson (1980) used flow-through boxes placed directly in streams to test the effects of predator chemical cues on mayfly settling behaviour. Significantly fewer mayflies settle on benthic substrates in a downstream plume of predator odour than settle in control treatments or where predators can only be detected visually. Settlement by barnacle larvae (*Balanus glandula*) in the field is significantly reduced on tiles that had been occupied by the predatory whelk *Nucella lamellosa* (Johnson & Strathmann, 1989). However, there is also significantly less settlement when tiles are treated with mucus from an infrequent predatory limpet and from the brown alga (*Fucus distichus*), so this may simply represent avoidance of all foreign proteins.

Some adult organisms must make habitat choices when they are nearing time for oviposition. Such responses are also avoidance responses, but adults appear to be avoiding habitats that would be risky to their offspring and not necessarily because the adults themselves are at risk. Several studies have noted that prey avoid ovipositing in sites that contain predators (*e.g.*, Chesson, 1984; Resetarits & Wilbur, 1989; Kats & Sih, 1992), but only two studies have linked the changes in oviposition behaviour to predator chemical cues. Fewer aquatic larvae of both mosquitoes (*Anopheles punctipennis*) and phantom midges (*Chaoborus flavicans*) are found in pools that contain caged bluegill sunfish than in control pools (Petranka & Fakhoury, 1991). Since the fish were not visible and cage mesh was too small to allow insects to enter (no direct predation), adult mosquitoes and midges likely avoid ovipositing in pools that contain chemical cues of predatory fish. Fewer mosquito larvae are also found in pools that contain caged frog tadpoles; however, midges apparently do not respond to tadpoles. Thus, mechanical cues alone (the movements of nonpredatory tadpoles) are not enough to produce changes in the oviposition behaviour of midges.

Bicolor damselfish (*Stegastes partitus*) females mate repeatedly during a reproductive cycle. They also tend to show nest site fidelity, laying their eggs at the same site during each spawning. Knapp (1993) found that females avoid nest sites from which oophagous brittlestars (*Ophiocoma echinata*) had removed previous broods. Using cages that prevented visual detection, Knapp found that female damselfish avoid sites that contain caged brittlestars. Thus, female damselfish presumably use chemical cues to avoid potentially risky nest sites.

Use of refugia

One special way to avoid or escape from predators is to hide or take refuge. While many types of prey behaviour offer refuge from predation (*e.g.*, aquatic prey leaving the water, burying) this section reviews the few studies that have documented increased use of physical refugia in response to predator chemical cues. Prey entering a refuge are often less visible to hunting predators and are typically in sites that are not accessible to predators.

In laboratory experiments, Wahle (1992) found that small (carapace length 9-15 mm) American lobsters (*Homarus americanus*) significantly increase shelter use in response to water-borne chemicals from a predatory sculpin. In both laboratory and field experiments, Petranka, Kats & Sih (1987) found that grey treefrog tadpoles respond to fish chemical cues by spending significantly more time hiding under opaque plexiglas plates than they did in control treatments. Since that study, several more species of both frog and salamander larvae have been found to increase refuge use in response to fish cues (Kats, Petranka & Sih, 1988). While there are several mechanisms that aquatic amphibians might use to detect chemical cues (*e.g.*, skin receptors, taste, olfaction), Kats (1988) found that salamander larvae with temporarily plugged external nares do not respond to predator chemical cues, indicating that the larvae are relying primarily on olfaction.

Reduced activity

Although many prey are known to become inactive or inconspicuous when they detect predators (Cott, 1940; Edmunds, 1974; Lima & Dill, 1990), studies have rarely determined the stimuli that promote this inactivity. Several species of stream dwelling crustaceans respond to predator cues by becoming less active. Benthic isopods (*Lirceus fontinalis*), for example, become inactive in response to chemical cues from predatory green sunfish (*Lepomis cyanellus*) (Holomuzki & Short, 1988; 1990), and amphipods (*Gammarus sp.*) exhibit a similar decrease in activity in response to a variety of fish species (Williams & Moore, 1982; 1985; Andersson *et al.*, 1986; Holomuzki & Hoyle, 1990). Aquatic midge larvae (*Chironomus tentans*) move significantly less in the presence of sunfish chemical cues (Macchiusi & Baker, 1992) and mosquito larvae show similar responses to odours from the predatory hemipteran *Notonecta undulata* (Sih, 1986). In laboratory experiments, Williams (1986) found that larvae of one species of stonefly (*Phasganophora capitata*) decrease movement when exposed to trout (*Oncorhynchus mykiss*) odour, while those of another species (*Paragnetina media*) increase movement.

Several studies have suggested that reduced activity in response to predator cues in the laboratory translates into altered drift activity of invertebrates in natural streams (Williams and Moore, 1982; Andersson *et al.*, 1986; Holomuzki & Short, 1990; Holomuzki & Hoyle, 1990). Williams & Moore (1982) and Andersson *et al.* (1986) found that amphipods (*Gammarus*) show significant reductions in drift when fish are introduced into laboratory tanks and similar reductions when fish exudates are added. In field experiments, Holomuzki & Short (1990) found that the presence of caged fish causes significant reductions in isopod drift at night. Amphipods show only slight reductions in nighttime drift in response to caged fish (Holomuzki & Hoyle, 1990).

Reduced activity and immobility responses would presumably be most effective for predators that are primarily visual hunters or those that key in on vibration or noise. Coho salmon juveniles decrease their activity when exposed to odours of visually hunting common mergansers (*Mergus merganser*) (Martel & Dill, 1993) and starry gobies (*Asterropteryx semipunctatus*) move less when they detect chemical cues from the highly visual lizardfish (*Synodus variegatus*) (Smith, 1989). Tadpoles of the tailed frog (*Ascaphus truei*) are significantly less active when exposed to water conditioned with cues from predatory Pacific giant salamanders (*Dicamptodon ensatus*) and introduced brook trout (*Salvelinus fontinalis*) than in control treatments (Feminella & Hawkins, 1992). Thoen, Bauwens & Verheyen (1986) and VanDamme *et al.* (1990) report that common lizards (*Lacerta vivipara*) typically alternate basking and inactivity with bouts of activity and even running. However, when chemical cues from predatory snakes are present, lizards alternate between inactivity and movements that the authors describe as "slow motion."

In 1920, Griffith found that white laboratory rats huddle together and become inactive when exposed to odours of domestic cats. Cattarelli (1982a,b) found that rats (*Rattus norvegicus*) increase the amount of time spent hiding and become immobile when exposed to air odourized with fox (*Vulpes vulpes*) feces (diet not reported). Courtney, Reid & Wasden (1968) found that rats proceed through a maze more slowly after a cat had walked through it than in control treatments. Rats do not slow down when the maze is sprayed only with a strong deodorant, suggesting that the rats are not slowing in response to novel odours in general. Dieterlen (1959) noted that Syrian hamsters (*Mesocricetus auratus*) respond to odours of dogs and cats with a variety of behaviours. Hamsters occasionally respond by increasing threat and aggressive displays, avoiding the odour source, or becoming inactive.

CHANGES IN FEEDING BEHAVIOUR

Given that organisms often respond to risk by eliminating or minimizing conspicuous actions or behaviours, it follows that some prey will reduce feeding when predator odours are detected. We assume that many other responses to predator odours (*e.g.*, avoidance, increased hiding, reduced activity) also result in alterations of prey feeding behaviours; however, only a few studies have examined feeding behaviour directly.

It is not obvious that the feeding behaviour of slow moving prey increases their susceptibility to predation. Yet, as discussed earlier, marine gastropods (*Nucella lamellosa*) feed less and grow less in the presence of crab (*Cancer spp.*) odours (Palmer, 1990). Palmer attributed the reduction in growth and feeding to both a reduction in snail activity and a predator cue induced switch to feeding on smaller prey. He hypothesizes that smaller prey have shorter handling times and thus, snails shorten the time exposed to foraging crabs. Similarly, the copepod *Diaptomus tyrrelli* responds to chemicals from a second copepod species (*Epischura nevadensis*) by reducing filter feeding by 60% (Folt & Goldman, 1981). *Epischura* is both a competitor and predator of *Diaptomus*. Folt & Goldman suggest that the reduced feeding in *D. tyrrelli* may be a result of allelopathic interference from *E. nevadensis*, or simply a product of the avoidance behaviour demonstrated by *D. tyrrelli*. In laboratory studies, Short & Holomuzki (1992) found that isopods (*Lirceus fontinalis*) move less when exposed to chemical cues from predatory fish (*Lepomis cyanellus*). This reduction in movement probably contributes to the significant reduction in leaf shredding by the isopods.

Several studies on the responses of mammalian prey to predator chemical cues indicate reductions in prey feeding (*e.g.*, Melchiors & Leslie, 1985; Sullivan & Crump, 1984; 1986b; Pfister, Müller-Schwarze & Balph, 1990; Merkens, Harestad & Sullivan, 1991; also see earlier discussion on avoidance behaviours). However, these changes in feeding behaviour only indicate that prey avoid food that has been contaminated with predator chemical cues or food that is closely associated with those cues. Thus, it is difficult to know whether prey are simply avoiding contaminated food or attempting to remain inconspicuous in order to avoid a potential nearby predator. Swihart, Pignatello & Mattina (1991) and Swihart (1991) used predator odours to alter the foraging behaviour of woodchucks (*Marmota monax*) and white-tailed deer (*Odocoileus virginianus*), respectively. When tubes of predator urine are attached to small trees there is a significant reduction in browse damage. Woodchucks and deer do not avoid plants treated with rabbit or human urine, suggesting that the response is not simply an avoidance of novel odours or of contaminated food. Antelope (*Raphicerus melanotis* and *Sylvicapra grimmia*) do not reduce feeding on plants treated with leopard (*Panthera pardus*), caracal (*Felis caracal*), laboratory rat or domestic sheep urine (Novellie, Bigalke & Pepler, 1982).

AGGREGATION

Schooling and shoaling behaviours of fish and invertebrates are typically thought to offer some degree of protection from predators (Bertram, 1978; Pitcher, 1986). Although the effects of predator presence on these behaviours have been studied in great detail (see for example Pitcher, 1986; Magurran & Higham, 1988; Pitcher, Lang & Turner, 1988), only two studies have examined the effect of predator chemical cues on schooling behaviour. Strand & Hamner (1990) found that schools of Antarctic krill (*Euphausia superba*) disperse when the school encounters nitrogenous waste from vertebrate predators (human and giant petrels). School dispersion is not what one would predict when predators are encountered, and the authors suggest that the school break-up is an adaptive response to high levels of metabolic by-products and not necessarily an antipredator behaviour *per se*. However, if predators are capable of consuming entire schools or shoals, dispersion might be a good defense strategy.

Minnows (*Phoxinus phoxinus*) continue to feed when first exposed to odours of a natural predator (*Esox lucius*) (Magurran, 1989). However, when chemical cues from injured conspecifics are introduced with predator chemical cues, minnows stop foraging and begin to school. Subsequent exposures to predator chemical cues alone are sufficient to produce schooling behaviour. Minnows (*P. phoxinus*) collected from naturally occurring shoals show tighter school cohesion when exposed to pike chemical cues than groups of minnows unfamiliar with each other (Chivers, Brown & Smith, 1995b). Familiar individuals also exhibit more dashing behaviour, a known antipredator response, than groups of unfamiliar individuals.

DEFENSIVE BODY POSTURING

Some organisms respond to chemical cues by assuming body postures that decrease vulnerability to predation or that are preparatory for escape. Keyhole limpets, for example, respond to chemical cues from predatory sea stars (*Pisaster ochraceus*) by extending mantle tissue over their shell (Margolin, 1964). Sea stars withdraw their tube feet when they contact the mantle tissue and predation is thus inhibited.

Eublepharid gecko lizards orient their tail toward approaching predators (Dial & Fitzpatrick, 1981): the tail is elevated from the normal horizontal position and directed toward the predator. This behavioural display likely misdirects predator attack toward the tail; tails autotomize when attacked and the lizards frequently escape (Dial & Fitzpatrick, 1981). Geckos also perform tail displays when presented with cotton swabs that have been rubbed on snake predators (Dial, Weldon & Curtis, 1989; Dial, 1990). Tail displays are frequently followed by rapid fleeing behaviour and vocalizations.

Some snakes are also known to assume defensive body postures in response to predator chemical cues. Cowles (1938) found that rattlesnakes (*Crotalus spp.*) elevate the middle portion of their body ("body bridging") in response to chemicals of both kingsnakes (*Lampropeltis spp.*) and spotted skunks (*Spilogale phenax*). Responses to kingsnakes are likely adaptive, since kingsnakes are known to feed on other reptiles, but the significance of responses to cues from spotted skunks is not entirely clear. Sidewinder rattlesnakes (*Crotalus cerastes*) also body-bridge in response to kingsnake odours (Bogert, 1941). In fact, a large number of crotaline (Crotalinae) snakes exhibit defensive body postures in response to kingsnake and other ophiophagous snake chemical cues (Weldon & Burghardt, 1979).

Alarm signaling

While a variety of behaviours might be interpreted as signaling alarm to conspecifics (*e.g.*, rapid or frenetic fleeing, defensive body postures), only two studies have noted more typical alarm behaviours in response to predator chemical cues. Rodents are known to drum their rear feet in response to predator chemical cues (*e.g.*, Randall & Stevens, 1987), and one study has noted the behaviour specifically in response to predator odours. Richardson (1942) reported that wood rats (*Neotoma albigula*) drum their feet in response to chemical cues from garter snakes (*Thamnophis spp.*). Foot drumming may intend to signal the predator that it has been seen, or it may function as a warning for nearby conspecific prey. Caine & Weldon (1989) found that tamarins vocalize more when exposed to chemical cues from margays than when they are exposed to chemicals from other mammalian predators. They suggest that the alarm call is most important in this situation because margays are more arboreal than other predators and, thus, more of a threat to the tree-dwelling tamarins.

Increase in sensory/detection behaviour

Although it would be difficult to assess whether many organisms respond to predator cues by increased visual alertness or by increased cue uptake, some organisms exhibit conspicuous behaviours which indicate changes in their rate of sampling the environment. For example, marsh periwinkles show a marked increase in the rate of tapping the cephalic tentacle to the substrate after exposure to predator chemical cues (Dix & Hamilton, 1993). However, the authors did not clearly establish whether the increase in tentacle tapping was directly related to predator cues or simply a by-product of the increase in locomotion speed that accompanied this response.

Several studies have noted significant increases in reptilian tongue-flicking after exposure to predator odours (*e.g.*, Weldon, 1982; Thoen, Bauwens & Verheyen, 1986; Cooper, 1990; Weldon, Ford & Perry-Richardson, 1990; VanDamme *et al.*, 1990). However, water moccasins (*Agkistrodon piscivorous*) tongue-flick less when placed into a tank that previously contained a predatory kingsnake (*Lampropeltis getulus*) than when placed into a tank that previously held a non-predatory hognose snake (*Heterodon nasicus*) (Chiszar *et al.*, 1978).

Red-bellied tamarins spend more time sniffing the air and scanning their surroundings when exposed to methylene extract of predator feces than when exposed to extracts from non-predatory animals (Caine & Weldon, 1989). California ground squirrels (*Spermophilus beecheyi*) sniff the air significantly more often when predatory rattlesnakes and gopher snakes are presented to them in perforated plastic bags than when the snakes are in sealed bags (Hennessy & Owings, 1978).

Physiological responses

Several studies report physiological responses of prey to predator chemical cues; however, the adaptive value of the response is not always readily identified. That there is some type of physiological change in prey when exposed to predator chemical cues indicates that prey have the mechanisms necessary for chemosensory detection of predators and are likely capable of an array of antipredator behaviours. Given that there is such a fine line between physiological responses and behavioral responses, we have included these studies in Table II.

Authors who have monitored physiological parameters in response to predator odours have reported a variety of responses. Bengtsson (1982) found that isopods significantly increase respiration rate in response to nonvolatile exudates from predatory amphipods. In addition, when isopods are presented with cues from both conspecifics and amphipods there is a significant increase in exudation of free amino acids. Rats and mice increase defecation when exposed to the odours of snake predators (Weldon, Divita & Middendorf, 1987) and to fox feces (Cattarelli & Chanel, 1979).

Cowles & Phelan (1958) monitored rattlesnake heart rate in response to "neutral odours", kingsnake odours, and normal butyl mercaptan which is found in skunk musk. Heart rates are unaffected by neutral odours; however, kingsnake odour and butyl mercaptan cause a sharp rise in heart rate. Chabot, Gagnon & Dixon (1996) found similar increases in heart rates in wapiti (*Cervus elaphus canadensis*) when they were exposed to gland secretions, feces or urine of mammalian carnivores.

Deermice (*Peromyscus maniculatus*) show a decreased sensitivity to painful thermal stimuli (analgesic response) when exposed to the combined odour and sound of short-tailed weasels (*Mustela erminea*) (Kavaliers, 1990), but since the predator could also be heard, the change in pain tolerance cannot be unequivocally attributed to olfactory cues.

One study (Rehnberg & Schreck, 1987) demonstrates that prey fish (juvenile coho salmon) respond to predatory fish cues with elevated plasma cortisol. However, juvenile salmon show the same physiological response when exposed to chemical cues from nonpredatory fish. Some mammals also respond to predator chemical cues with increased plasma hormones. For example, rats (*Rattus norvegicus*) exposed to fox feces or molecules from fox feces have elevated plasma corticosterone levels (Vernet-Maury, 1980; Vernet-Maury, Polak & Demael, 1984).

LIFE-HISTORY RESPONSES

Some of the more remarkable predator chemical cue induced changes occur in prey life-histories (Table III). Washburn *et al.* (1988) found that water-borne cues from predatory larval mosquitoes cause free-living protozoan prey (Ciliophora: Tetrahymenidae) to transform into obligate parasites that attack the mosquitoes. When protozoans are placed into water that has previously contained mosquito larvae their daughter cells attack newly introduced mosquito larvae by encysting on the larval cuticles. They enter the hemocoel of the mosquito, multiply, and ultimately kill their host and former predator.

Crowl & Covich (1990) found that stream snails (*Physella virgata*) show rapid growth and delay reproduction in the presence of cues from crayfish actively foraging on conspecific snails. However, cues from crayfish alone are not enough to stimulate the delay in snail reproduction and they did not examine whether alarm cues from injured snails would trigger the response. Daphnids (*Daphnia galeata*) become reproductively mature at smaller sizes when reared in water containing cues from predatory fish (*Rutilus rutilus*) than in control water (Máchacek, 1991). In addition, experimental daphnids tend to produce smaller eggs than control animals. Stibor (1992) found similar results using *Daphnia hyalina* and predatory fish (*Leuciscus idus*), and also found that *Daphnia* exposed to fish cues have higher relative reproductive investment than control animals. Máchacek (1991) suggests that the smaller sizes of adults might be an adaptive response to visually hunting fish predators. It has been suggested that life-history changes might be connected to costs of developing induced morphological defences, that is, prey might reproduce at smaller sizes because they are trading off body size for a spine or other defensive morphology. However, Lüning (1994) found that life history changes in *Daphnia pulex* (in response to *Chaoborus* chemical cues) can arise independent of morphological defences and are therefore not simply a cost of building a morphological defence.

Sih & Moore (1993) report that salamander embryos (*Ambystoma barbouri*) hatch later (and at larger size) in laboratory tubs that contain chemical cues from predatory planaria than in tubs that do not. Since planaria are predators on small, newly hatched larvae (Petranka, Kats & Sih, 1987), a delay in hatching presumably allows larvae to grow and develop in order to increase their chances of escape.

Just as in the case of morphological defenses, behavioural defenses can also translate into reductions in growth and these may have life-historical consequences. Skelly (1992) found that tadpoles (*Hyla versicolor*) respond to caged predatory *Ambystoma* larvae by reducing movement. A field study showed that tadpoles grown in the absence of the predator were 54% heavier than tadpoles grown with the predator. Given that the predator was placed into a screen enclosure, cues other than chemical might have been important in mediating the reduction in growth, although *H. versicolor* tadpoles are known to alter their behaviour in response to predator chemical cues alone (Petranka, Kats & Sih, 1987). In a similar experiment, damselfly larvae (*Ischnura*) fed significantly less when in the presence of a caged predatory aquatic bug (*Notonecta*) than when by themselves (Heads, 1986). Heads estimated that the reduction in feeding would translate into a 4-18% decrease in larval developmental rate, and slow development means a longer larval period and potentially an extended period of exposure to aquatic predators. Thus, reduced growth is unlikely to be an adaptive response to predator odour. Recently, Ball & Baker (1996) found that midge larvae (*Chironomus tentans*) are smaller at emergence and have lower fecundity when exposed to chemical cues from predatory fish (*Lepomis gibbosus*) than larvae in control treatments. The authors concluded that smaller size did not result from increased developmental rate (and thus a minimization of time spent with fish), but is best viewed as a cost of larvae behaviorally avoiding fish predators.

In many invertebrates, the timing of molt is an important life-history event, influencing individual growth and reproductive rates, but molting is risky, since a freshly molted individual is more vulnerable to predators (Soluk, 1990). The xanthiid crab *Leptodius sangineus* responds to the presence of the odour of its predator (the swimming crab, *Thalamita crennata*) by delaying its molt in the laboratory; it seems to be especially responsive to increases in cue strength, rather than to absolute level of cue strength *per se* (Harvey, 1993).

Discussion

To this point we have noted a wide variety of responses by prey to predator chemical cues. Responses have been detected in many different types of animals, but the majority of the responses have been recorded in freshwater and marine invertebrates, fish, and mammals. While there is an abundance of publications recording prey responses to predator cues, we also note that very few studies attempt to integrate their results into a larger context of chemically mediated antipredator defense. In the rest of the paper we will examine the evolutionary implications of responding to predator chemical cues.

ADVANTAGES AND DISADVANTAGES OF CHEMICAL CUES

Clearly there are some significant advantages for prey able to detect predators via chemical cues, particularly when other cues are unavailable. In turbid water, prey able to detect predator odours would certainly be better suited to deal with predators than prey that rely solely on visual detection. Many species of fish that inhabit turbid waters have well-developed chemosensory systems (*e.g.*, ictalurids, some cyprinids; Moyle & Cech, 1988; Hara, 1992). While most discussions have focused on the necessity of chemical detection mechanisms for locating food, homing or pheromone communication (Hara, 1992), selection for predation risk assessment would also provide similar abilities. Organisms that inhabit cluttered or physically complex habitats would also benefit by detecting predator chemical

TABLE III. Life history responses to predator odor

Prey	Predator	Response	Author
KINGDOM PROTISTA			
Ciliate, *Euplotes octocarinatus*	turbellarian, *Stenostomum sphagnetorum*	Increase in generation time	Kusch & Kuhlmann (1994)
KINGDOM ANIMALIA			
Phylum Rotifera			
Brachionus calyciflorus	Rotifer, *Asplanchna*	Higher population growth rate (reduced threshold food concentration for reproduction)	Stemberger (1990)
Phylum Mollusca			
CLASS GASTROPODA			
Physella virgata	Crayfish, *Oronectes virilis*	Rapid growth, inc. age & size at maturity	Crowl & Covich (1990)
Phylum Arthropoda			
CLASS CRUSTACEA			
Cladoceran, *Daphnia*	*Chaoborus*, *Notonecta* and bluegill sunfish, *Lepomis macrochirus*	Changes in clutch size, body size & development time	Dodson (1989); Dodson & Havel (1988)
Daphnia carinata	*Notonecta gratus*	Longer instar duration, delayed age at reproduction, smaller eggs, later broods have larger clutch size	Barry (1994)
Daphnia galeata	Roach, *Rutilus rutilus*	Slower growth, and earlier reproduction; smaller size at first reproduction; larger relative clutch size	Máchacek (1991)
D. galeata	Roach, *R. rutilus*; perch, *Perca fluviatilis*	Reduced juvenile length increments; earlier maturation; larger clutches of smaller eggs	Máchacek (1993)
Daphnia hyalina	Fish, *Leuciscus idus*	Inc. allocation to reproduction; earlier reproduction at smaller size	Stibor (1992)
D. hyalina	Fish, *Leuciscus idus*, and bug, *Notonecta glauca*	Reproduction at smaller size	Stibor & Lüning (1994)
D. hyalina	*Chaoborus flavicans*	Reproduction at larger size	Stibor & Lüning (1994)
Daphnia galeata x *hyalina* hybrid	Perch, *Perca fluviatilis*	Ealier maturation, larger size of first clutch, smaller neonates	Reede & Ringleberg (1995)
Daphnia lumholtzi	Bleak, *Leucaspius delineatus*	Lower size at first reproduction	Tollrian (1994)
Daphnia magna	Fish, *Leucaspius delineatus*	Smaller size; smaller size and age at first reproduction; smaller offspring; larger clutches	Weider & Pijanowska (1993)
D. magna	Fish, *L. delineatus*	Reduced growth; inc. investment in reproduction; larger clutches; smaller eggs	Dawidowicz & Loose (1992)
Daphnia pulex	*Chaoborus americanus*	Fewer, but larger offspring, which delayed first reproduction	Lüning (1992)
D. pulex	*Notonecta glauca*	More & smaller offspring; earlier maturation	Lüning (1992)
D. pulex	*Chaoborus americanus*	Delayed maturity (some clones)	Spitze (1992)
D. pulex	*C. americanus*	Delayed first reproduction	Black & Dodson (1990)
D. pulex	*C. americanus*	Delayed maturity	Black (1993)
D. pulex	*C. flavicans*	Delayed maturity; smaller size at maturity, reduced fecundity	Lüning (1994)
D. pulex	*Notonecta undulata*	Rapid juvenile growth	Black (1993)
D. pulex	Fish, *Lepomis gibbosus*	Smaller size at reproduction and increased clutch size	Engelmayer (1995)
D. pulex	*Chaoborus obscuripes, C. crystallinus Mochlonyx sp., Dytiscus, Notonecta*	Delayed reproduction, smaller clutch size, less growth	Repka, Ketola & Walls (1994)
CLASS INSECTA			
Chironomus tentans	Fish, *Lepomis gibbosus*	Smaller size at emergence, dec. growyh and devpt. rates, lower fecundity	Ball & Baker (1996)

(continued on next page)

TABLE III. (concluded)

Prey	Predator	Response	Author
Phylum Chordata, Subphylum Vertebrata			
CLASS AMPHIBIA			
Salamander	Fish	Delayed hatching	Moore, Newton & Sih (1996)
Salamander, *Ambystoma barbouri*	Flatworm, *Phagocotus gracilis*	Delayed hatching of eggs (at larger size)	Sih & Moore (1993)
CLASS MAMMALIA			
Bank vole, *Clethrionomys glareolus*	Mustelid	Suppression of breeding in females	Ylönen & Ronkainen (1994); Mappes & Ylönen (1992)
Vole, *Clethrionomys spp.*	Mustelid	Reduced litter weight and delayed maturation	Heikkila *et al.* (1993)
Field vole, *Microtus agrestis*	Mink, *Mustela vison* & least weasel, *M. n. nivalis*	Supression of breeding	Koskela & Ylönen (1995)

cues, as would prey that frequently encounter cryptic predators or predators that rely on ambush tactics. Nocturnal prey might also be under strong selection to detect predator chemicals. In addition, prey that rely on chemical indicators for predator avoidance can presumably assess risk from the safety of their refuge. Organisms that rely primarily on visual or mechanical assessments might have to leave the safety of their refuge to gather new information about the presence or absence of a predator and thereby risk being captured. However, chemical assessment might also lead to excessively conservative estimates of risk if prey continue to hide despite the absence of the predator.

Selection for chemical detection of predators by prey is presumably dependent upon characteristics of the predator, *i.e.*, chemical information about slow moving predators or predators that are confined to certain areas should be accurate and be an indication that the local area is still risky. For example, Sih, Kats & Moore (1992) found that salamander larvae (*Ambystoma barbouri*) use chemical cues to detect predatory fish. One might think that chemical detection of fast-moving fish would not be all that helpful to the small (0.4-1.0 g) rather slow larvae, given that fish swimming throughout a stream could likely encounter larvae before being detected chemically. But in this system, fish are confined to relatively deep stream pools (> 1 m) and are not free to move widely throughout the stream. Thus, when salamander larvae drift into fish pools they can use chemical cues as an immediate indicator of risk and behave differently than when they drift into fishless pools (Figure 1). Chemical information about fast-moving and wide-ranging predators may not be as reliable, given that chemical cues of fast-moving predators probably linger long after the predator is gone.

Chemical detection of a predator indicates to prey that a given area was risky at some point in time; however, it does not necessarily indicate present risk. Given the lost opportunity costs to hiding (*e.g.*, less time for foraging, searching for mates), prey that rely heavily on chemical cues for risk assessment probably suffer hiding costs even after the predator has left the area. Depending on air and water currents and the volatility of the cue, prey might frequently stay in hiding much longer than is actually necessary. For example, Bollens & Frost (1989) note that marine copepods exhibit diel migrations for 2-3 days even after being removed from the presence of the predator and, *Chaoborus* behave as if a fish predator was present for 15 days after its removal (Dawidowicz, Pijanowska & Ciechomski, 1990). In addition, even when predators remain in the area, the exact location of the predator might be difficult to assess via chemical cues. Holomuzki and Hatchett (1994) have suggested that isopods that respond to fish cues over short term exposures stop responding to fish cues during extended exposures (possible habituation) because of costs associated with predator avoidance.

Organisms with the ability to assess risk via chemical cues might be able to use chemical gradients to provide better spatial resolution of predator location. Few studies have examined the abilities of prey to detect predator chemical cue-gradients or determined whether prey behave differently when exposed to varying concentrations of predator cues. We found only three studies that clearly demonstrated increasing responses of prey to increasing concentrations of predator chemical cues (Loose & Dawidowicz, 1994; Horat & Semlitsch, 1994; McKelvey & Forward, 1995).

On the other hand, the very fact that odour cues persist in the absence of the predator that produced them may be one of their major advantages. It is possible for prey to obtain information on the likelihood of predator presence in an area, based on their presence there in the past ("the ghost of predation future"). Of course, the value of this information will depend on whether predators revisit areas, and on

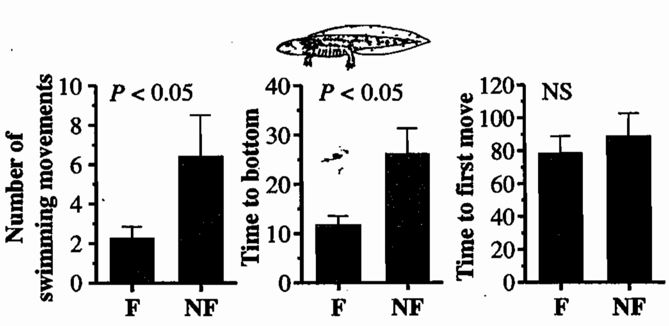

FIGURE 1. Behavior of salamander larvae (*Ambystoma barbouri*) immediately after they were first dropped into fish (F) and fishless (NF) pools. Shown are means and 1 SE. Comparaisons were made using a Mann-Whitney *U*. NS = not significant at the 0.05 level. From Sih, Kats & Moore (1992).

their frequency of visitation compared to the rate of dissipation of the chemical cue. In some situations (*i.e.*, long time intervals between visits) the presence of a chemical cue from a mobile predator may actually signal a low risk.

CUE SPECIFICITY: PREDATORS *VERSUS* NON-PREDATORS

Most studies on chemically-mediated predator avoidance do little to describe the cue itself. Some authors have suggested that prey respond to general chemical signals, but a significant disadvantage to responding to a general signal is the costs associated with responding to non-predatory species. Several studies have addressed the interesting evolutionary questions regarding prey responses to predators compared to similar non-predatory species.

Two studies on gastropods have demonstrated that prey can discriminate between predators and non-predators. Rocky shore gastropods (*Nucella lamellosa*) avoid effluent from predatory crab species, but not effluent from non-predators (Marko & Palmer, 1991). Marsh periwinkles (*Littoraria irrorata*) increase locomotion speed when touched with a swab that contains chemical cues from predatory whelks (Dix & Hamilton, 1993). They also increase speed in response to mucus from other neogastropods, even though they rarely or never encounter them; however the escape response to the frequent predator (crown conch, *Melongena corona*) is significantly stronger than the responses to the other species (Figure 2). Periwinkles do not respond to cues from non-predatory sea hares or scallops. Herbivorous snails, *Tegula funebralis*, crawl out of the water in response to chemical cues from five species of predatory sea stars but do not respond to non-predatory sea stars (Yarnall, 1964). Similarly, sea urchins (*Stronglycentrotus droebachiensis*) move away from chemical stimuli from predatory rock crabs but do not respond to non-predatory green crabs (Scheibling & Hamm, 1991). Juvenile salmon (*Oncorhynchus kisutch*) avoid chemical cues from predatory squawfish (*Ptychocheilus oregonensis*) but do not avoid chemicals from non-predatory largescale suckers (*Catostomus macrocheilus*; Rehnberg & Schreck, 1987). In contrast to the above examples, some prey apparently do respond to general cues. For example, Williams & Moore (1985) found that amphipods (*Gammarus pseudolimnaeus*) decrease activity when exposed to chemical cues from both predatory and non-predatory fish, and hypothesized that amphipods are responding to a very basic fish chemical, such as mucus. Barnacle larvae show a reduction in settling on substrates that contain mucus from a predatory whelk (Johnson & Strathmann, 1989), but respond similarly to mucus from a brown alga (*Fucus distichus*) and from a non-predatory limpet.

Lizards (*Lacerta vivipara*) show increased tongue-flicking in response to two predatory snakes and one non-predatory snake, compared to controls (Thoen, Bauwens & Verheyen, 1986), but tongue-flicking is highest in response to the two predatory species. In addition, defensive postures and slow body movements only occur in response to odours from the predatory snakes. However, Cooper (1990) pointed out that the previous study may be flawed given that cues were always presented to the same lizards in order, *i.e.*, non-predatory cues were always presented to the lizards last and lizards may have become habituated to snake cues.

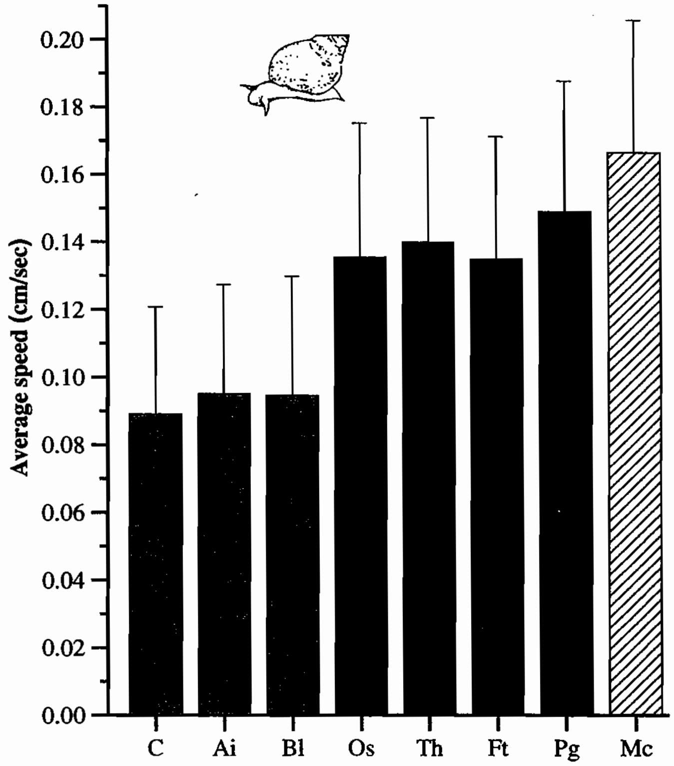

FIGURE 2. Average speeds of marsh periwinkles (*Littoraria irrorota*) after exposure to seawater (C) or mucus from one of seven molluscan species. Nonpredators = Ai, B1. Allopatric predators = Os, Th, Ft, Pg. Sympatic predator = Mc. Shading patterns indicate signifiant groups according to Duncan's Range test. Shown are means and 1 SD. (Ai = *Argopecten irradians*, B1 = *Bursatella leachii*, Os = *Oliva sayana*, Th = *Thais haeomostoma*, Ft = *Fasciolaria tulipa*, Pg = *Pleuroploca gigantea*, Mc = *Melongena corona*.). From Dix & Hamilton (1993).

Using a random design, Cooper (1990) demonstrated that adult male skinks, *Eumeces laticeps*, tongue-flick more in response to chemical cues from predatory kingsnakes than to cues from non-predatory hognose snakes or odourless controls. Similarly, rattlesnakes (*Crotalus viridis*) reduce exploratory behaviour when exposed to chemical cues from predatory kingsnakes but increase exploratory behaviours in the presence of chemicals from harmless hognose snakes (Chiszar *et al.*, 1978). On the other hand, young corn snakes (*Elaphe guttata*) show no significant differences in tongue-flicking in response to ophiophagous and non-ophiophagous snakes (Weldon, Ford & Perry-Richardson, 1990). Jackson (1990) demonstrated that musk turtles (*Sternotherus sp.*) avoid water that contains chemical cues from predatory alligator snapping turtles (*Macroclemys temmincki*) but do not avoid cues from non-predatory pond turtles (*Pseudemys sp.*).

Snowshoe hares (*Lepus americanus*) stop feeding on lodgepole pine seedlings when vials of urine from predatory wolverines (*Gulo gulo*) are attached to the trees (Sullivan, 1986). However, hares continue to feed on plants with deer (*Odocoileus hemionus*) urine attached to them. Hares are not simply responding to novel odours or avoiding fouled food, but appear to avoid cues specific to wolverines.

In summary, prey frequently respond more to chemical cues from predators than to cues from non-predatory organisms, but there are also several examples where prey do not appear to show differential responses to predator and non-predator cues. These counter examples are interesting and suggest possible alternative hypotheses: *i.e.*, (*i*) selection pressures from the predator are not as strong as might be presumed, (*ii*) the prey behaviour assayed might not be the correct behaviour to monitor or, (*iii*) non-predator and predator cues are so similar that prey are simply not able to differentiate the two.

TAXONOMIC GAPS

Two large groups of animals are conspicuously absent from this review; neither birds nor terrestrial insects have been widely reported to possess the ability to recognize the odours of their predators. This is particularly curious given that insects are well known for chemical communication, and many aquatic species do have the ability (Table I). Even birds have better olfactory capabilities than has previously been recognized (Kare & Mason, 1986; Clark, Avivola & Bean, 1993), but only one example has been reported in birds. Mason, Clark & Shah (1991) report that European starlings (*Sturnus vulgaris*) avoid food contaminated with ortho-aminoacetophenone, a component of the scent gland secretions of mustelid predators. We can think of only three possibilities for these apparent taxonomic gaps. First, it is possible that there is something about air as a medium (*e.g.*, turbulent mixing; high rate of diffusion) that makes it unsuitable as a reliable carrier of information about predation risk. Other terrestrial groups that rely on chemical cues typically detect cues either in relatively close proximity to the predator or to a contaminated substrate and are not detecting long distance aerial cues. Second, perhaps there may be more reliable and readily obtainable sources of information available to birds and insects (*i.e.*, visual range most often exceeds olfactory range). However, there would seem to be many cases where odour cues might provide the best or only source of crucial information, *e.g.*, when choosing nest or roost sites or foraging locations. Finally, and most likely, it may simply be that no one has investigated chemically-mediated predator detection in these taxa.

Recently, Hansson (1996) suggested that even plants can respond to the chemical cues of herbivores. He found that flagellated algae remained on substrates longer (and did not enter the water column) in habitats that contained cues of herbivorous *Daphnia magna* than in habitats that did not contain *Daphnia* cues. This study suggests that chemically mediated defensive behaviors should be examined more closely in the plant kingdom.

RISK ASSESSMENT: INFORMATION IN THE CUE

Only a few studies have addressed the specifics of the predator cue in mediating prey behaviour. For example, if predators are not uniformly risky to prey, prey might be expected to respond more strongly to individual predators that are riskiest. Sea urchins (*Strongylocentrotus purpuratus*) give stronger pedicellaria responses to water flowing over active predatory sea stars (*Pycnopodia helianthoides*) than over inactive sea stars (Phillips, 1978). The author hypothesized that the predator chemical originated from the tube feet of the sea star. Thus, a moving sea star was exposing far more tube foot surface area than an inactive sea star, and the prey would perceive higher concentrations of the cue. In addition, active sea stars are likely to be foraging and would certainly be more risky to prey than inactive sea stars. Mackie (1970a,b) identified a steroid glycoside (saponin) as the substance coming from the epidermis of sea stars that caused defensive behaviours in gastropods (*Buccinum undatum*), scallops (*Pecten maximus* and *Chlamys opercularis*) and brittle stars (*Ophiothrix fragilis*).

If prey respond to metabolic by-products from predators, predator diet may play a role in mediating the responses in some prey. The data on the effects of diet on prey responses provide mixed results. Marsh periwinkles (*Littoraria irrorata*) respond to sympatric and allopatric predatory crown conchs (*Melongena corona*) even though allopatric conchs could not have previously fed on marsh periwinkles (Dix & Hamilton,1993). However, brook trout avoid water coming from salmon that have been fed goldfish significantly more than water from salmon that have been fed mealworms (Keefe, 1992). Gelowitz, Mason & Smith (1993) found that brook stickleback (*Culaea inconstans*) allopatric to predatory pike (*Esox lucius*) decrease activity when exposed to chemical cues only from pike that had eaten conspecific sticklebacks. On the other hand, sympatric sticklebacks respond to pike cues regardless of whether the pike have eaten conspecifics or heterospecifics. Naive fathead minnows (*Pimephales promelas*) exhibit fright reaction to unfamiliar pike that had eaten conspecific minnows but did not respond to cues from pike that had eaten heterospecifics (swordtails, *Xiphophorous helleri*; Mathis & Smith, 1993a). Frog tadpoles (*Rana aurora*) show reduced movement when exposed to chemical cues from predatory newts (*Taricha granulosa*) fed conspecific frogs, but do not respond to newts that have been fed insects (Wilson & Lefcort, 1993). Mammalian prey, mountain beaver (*Aplodontia rufa*), house mouse (*Mus musculus*), deer mouse (*Peromyscus maniculatus*), and guinea pig (*Cavia porcellus*), avoid food contaminated with coyote urine (*Canis latrans*) more if the coyotes have fed on meat than if the coyotes have fed on fruit (Mason, Epple & Nolte, 1994; Nolte *et al.*, 1994). The authors suggest that prey cue in on sulfurous metabolites that are generated from meat digestion in predators. Chivers, Wisenden & Smith (1996) found that damselflies (*Enallagma spp.*) respond to cues from predatory pike (*Esox lucius*) that have fed on conspecific damselflies and fathead minnows (*Pimephales promelas*) but do not respond to pike fed mealworms. They suggest that damselflies might respond to pike that have eaten either damselflies or minnows because these prey are sympatric and probably share many of the same predators.

Howe & Harris (1978) have suggested that predatory nudibranchs (*Aeolidia papillosa*) give off an alarm pheromone (anthopleurine) after feeding on sea anemones (*Anthopleura elegantissima*); sea anemones withdraw sensitive body parts (tentacles and oral disc) much more frequently when exposed to nudibranchs that have recently fed on conspecific anemones than when the nudibranchs have been deprived of food. They further confirmed their hypothesis by noting that anemones also respond to chemical analogues of anthopleurine and by noting that levels of anthopleurine increase in nudibranchs after feeding on anemones.

Bengtsson (1982) found that amphipod prey have stronger responses to predatory isopods when predators have been exposed to prey cues than to predators that have not been so exposed. The author suggests that the predator is stimulated in some way by prey cues and is subsequently easier to detect by other prey individuals. Unfortunately, the study was not designed to differentiate between changes in predator stimulation and prey response to conspecific cues. While prey cues were passing over the predator, they were also continuing through the flow-through system to other prey organisms that were being monitored for responses.

Daphnia seem to have specific antipredator responses that depend on the type of predator that they are sensing (Watt & Young, 1994). When *Daphnia* detect chemicals from invertebrate predators (*Notonecta*) they alter their horizontal migration, and when they detect chemicals from predatory fish (*Carassius auratus*) they modify their vertical migration. Each of these shifts appear to be specific adaptive responses to the particular foraging habits of the predators.

Daphnia also seem to show differential morphological responses in response to predator diet (Grant & Bayly, 1981), developing protective crests when they are exposed to chemical cues coming from notonectids that have fed on either conspecific *Daphnia* or frog tadpoles, but showing little or no crest development in treatments where notonectids are starved. Crests are larger in treatments exposed to notonectids fed conspecifics than in treatments where notonectids are fed tadpoles.

COEVOLVED RESPONSES

Given that prey populations will experience different predation pressures when coexisting with different types of predators or different predator densities, it is not surprising that several studies have indicated population differences in response to predator chemical cues. Kats, Petranka & Sih (1988) found that larvae from stream breeding populations of salamanders (*Ambystoma texanum*) respond to odours of predatory green sunfish (*Lepomis cyanellus*) by increasing the amount of time spent in refuge. Larvae from ephemeral pond-breeding populations do not increase refuge use when exposed to fish odours. Selection pressures from predators contributed to the divergence of the two groups of salamanders, and the stream-breeders were subsequently described as a separate species (Kraus & Petranka, 1989). Mathis, Chivers & Smith (1993) found that fathead minnows (*Pimephales promelas*) sympatric to predatory northern pike (*Esox lucius*) decrease movement when exposed to pike chemical cues; allopatric minnows do not respond to pike chemical cues. Similarly, responses of whelks to predator cues vary from population to population; the strongest responses only result from cues of sympatric predators (Rochette, in prep.).

On islands off western Australia some populations of mice (*Mus domesticus*) are sympatric with fox and cat predators while other populations do not coexist with these predators (Dickman, 1992). In a field study, mice from populations sympatric with fox and cat predators avoid live-traps that had been treated with predator feces; mice from populations without predators show little or no avoidance of predator-treated traps. It is interesting that Dickman hypothesizes that predator-free mouse populations were founded from ancestral populations that coexisted with predators. Thus, the avoidance responses have apparently been lost over time, suggesting that there may be a cost to maintaining these antipredator behaviours.

Spitze (1992) recently noted that the *Chaoborus*-induced defenses in *Daphnia pulex* vary from genotype to genotype. Clones taken from four populations of *D. pulex* differ significantly in their expression of defensive neck teeth when exposed to *Chaoborus* extract. Thus, predator induced morphologies do not appear to be an all-or-nothing phenomenon.

INTRASPECIFIC VARIATION IN RESPONSE

There is significant evidence in the literature indicating that individuals within a species may differ in their responses to predator chemical cues. For example, responses to predator cues can change during ontogeny. Wahle (1992) found that small lobsters (*Homarus americanus*) respond to predatory sculpin (*Myoxocephalus anaeus*) chemical cues by spending increased time in shelter, whereas larger lobsters respond to predators with aggressive displays. He suggests that small lobsters can afford to restrict foraging to within shelters, whereas the energetic demands of large lobsters require that they forage more widely. In species with intraspecific predation, where small individuals are vulnerable to larger conspecifics, one might predict that ontogenetic shifts occur in response to adult odours. For example, adult male rodents are known to invade nests and kill the young of a prospective mate (Bruce effect). Rodent pups produce more vocalizations in the presence of female chemical cues than in the presence of male chemical cues and this has been interpreted as a possible mechanism for avoiding cannibalistic males (Lyons & Banks, 1982; Ostermeyer & Elwood,1983). As pups grow up, responses to adult cues should change. Elliott, Kats & Breeding (1993) found that California newt larvae (*Taricha torosa*) avoid the odours of predatory conspecific adults. Obviously, the response to conspecific adult odours changes as the larvae reach maturity since many newts are known to identify and assess mates via chemical cues (Verrell, 1986; Rowland, Robb & Cortwright, 1990). Kats *et al.* (1994) found that two-week-old newt larvae respond to chemical cues from adult conspecifics, but five-week-old larvae do not. The ontogenetic shifts in responses of prey to odours of conspecifics is virtually unstudied, but given the widespread prevalence of cannibalism we suspect that many organisms have similar ontogenetic shifts in response to conspecific cues.

In some species there appear to be differential responses to predator odours by males and females. Holomuzki & Short (1990) found that female isopods (*Lirceus fontinalis*) are significantly less active when chemical cues from predatory green sunfish (*Lepomis cyanellus*) are present in stream experiments than when cues are absent. Males do not reduce activity. Similarly, Weldon, Divita & Middendorf (1987) found that only female laboratory mice respond to snake cues (*Elaphe obsoleta*) with increased defecation. Males show no perceivable response to snake chemical cues. Females might respond more to predator chemicals than males because they might be more vulnerable to predators, particularly if gravid or pregnant females are slower or easier for predators to catch. Yet in other examples, males respond more than females to predator chemical cues. Traps with red fox (*Vulpes vulpes*) chemical cues are more often avoided by male wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) than by females (Dickman & Doncaster, 1984). The authors hypothesized that males of these species tend to be more active and visible to predators than females and would be most at risk of predation; thus, they should be more sensitive to predation risk.

Response to predator cues is also known to depend upon the context. Sih & Kats (1991) found that the presence or absence of available refuges influenced the response of salamander larvae (*Ambystoma barbouri*) to chemical cues from predatory fish. Salamander larvae were gently dropped into pools that contained fish cues. Pool bottoms either had refuges which larvae could crawl under or had no cover available. In situations where no refuge was available, larvae remained stationary significantly longer than in pools which contained refuges.

Chiszar *et al.* (1992) found that rattlesnakes perform a defensive "body-bridging" behaviour in response to cues from predatory kingsnakes when the rattlesnakes are in artificial burrows. Presumably, the body-bridging while in the burrow makes the rattlesnake more difficult for predators to grab and constrict. Rattlesnakes do not attempt to body-bridge in response to predator cues when they are outside of their burrows. Again, the response of the prey depends on the situation and surroundings when exposed to predator chemical cues. In these two studies there does not appear to be an "automatic" response to predator odours, but a response designed to be the most effective defense in a particular situation.

Very few studies have addressed the role of experience and learning in chemically mediated antipredator behaviours. Prey are often collected from the field and used in predator-prey experiments with little regard as to the individuals' history with predators. However, Neill (1990) looked at the responses of copepods that had been without predation pressure for four generations. In response to odours from predatory midge larvae, copepods begin a distinct diel vertical migration pattern that decreases their probability of contact with actively foraging midge larvae. Thus, no prior experience or exposure to the predator cues is necessary to induce the behaviour.

The earliest work on the role of experience in the development of responses to predator chemical cues was probably with fish. Goz (1941) and von Frisch (1941a) suggested that the response of fish to predator odour was a conditioned response. More recently, Magurran (1989) found that European minnows do not initially respond to the odours of predatory pike; however, if minnows are exposed to conspecific alarm odours in association with pike odours they respond to predator odours alone in subsequent trials. Magurran also noted that minnows develop a similar conditioned response to a non-predatory exotic fish, the cichlid (*Tilapia mariae*), but the response is not as strong as to the predatory pike. In a similar study, juvenile brook trout do not appear to have innate responses to predatory pike that have been fed goldfish. This is not surprising, since trout are non-Ostariophysians, and show no response to cyprinid alarm substance (Keefe, 1992). The brook trout did learn to respond to pike odours after being conditioned by electric shock. Naive fathead minnows (*Pimephales promelas*) learn to respond to pike (*Esox lucius*) chemical cues when paired with experienced conspecifics. Brook stickleback (*Culaea inconstans*) learned to respond to predator cues when paired with experienced heterospecific minnows and were able to transfer the fright response to other naive minnows (Mathis, Chivers & Smith, 1996). Learning and experience may be important in understanding why some studies report that prey show no response to predator cues (see for example Barnett, 1982).

A relatively unexplored area of investigation is the role of prey health in responses to predator odours. Kavaliers & Colwell (1995) found that mice (*Mus musculus*) that had been infected with an enteric protozoan parasite (*Eimeria vermiformis*) did not avoid cat odour as much as uninfected mice.

COUNTER ADAPTATIONS BY PREDATORS

If prey detect predators by their odour, and effectively avoid them, this should select for behaviours of predators to conceal such odours. However, few examples of this have been reported.

Given that feces are often the source of the predator odour, latrine behaviour might be viewed in this context; predators might selectively defecate in areas where they do not hunt. Possible examples include the common tern (*Sterna hirundo*), which has been reported to defecate more frequently on land than in its own fishing territory. Terns are, however, markedly less fastidious when flying over another bird's territory (Nisbet, 1983). Similar behaviour has been reported in shorebirds and several species of herons (Recher & Recher, 1972; Bayer, 1980), as well as in northern pike, *Esox lucius* (Brown, Chivers & Smith, 1995a; 1996). Some other eliminative behaviours, whereby animals avoid soiling their immediate surroundings, might have the effect of reducing cues for prey avoidance, although such behaviours are usually viewed as adaptations to avoid re-infection by internal parasites (Hart, 1990). Despite the apparent advantages of doing so, it may not always be possible for predators to cover their olfactory tracks. For example, many prey seem to respond to olfactory territory markers of carnivores such as weasels. The cost of reduced production of these signals, in terms of reduced efficiency of territory defense, may greatly outweigh the potential benefits from reduced prey avoidance. However, it is possible that a predator's metabolism is adapted to reduce odour production or the likelihood of producing chemical information for its prey.

Predators should also be selected to cover up their body odours in some way. Occasionally, this takes the form of chemical mimicry. Thus, the larval syrphid *Microdon albicomatus* synthesizes a cuticular hydrocarbon identical to that of its *Myrmica* ant prey (Howard, Stanley-Samuelson & Akre, 1990). This seems to deceive the worker ants, which allow the predators free access to their nest to consume the larvae. In addition to such olfactory mimicry, olfactory crypsis, whereby a predator covers up its own odour with the odour of its prey (a "wolf in sheep's aroma" tactic), or with some neutral environmental scent, has also been reported. For example, the parasitic larva of the wasp *Orasema* develops within colonies of its fire ant (*Solenopsis invicta*) hosts, and passively acquires its colony odour, allowing it to remain within the nest (Vander Meer, Jouvenaz & Wojcik, 1989).

Finally, in any situation in which the medium is moving in a certain direction it would benefit foraging predators to move in such a way that their odour is not carried towards their prey. Thus, terrestrial carnivores are often said to hunt upwind (but see Schaller, 1972). It would be interesting to know whether predators in streams (where responsiveness to chemical cues seems especially well developed) tend to work their way upstream when searching for prey. Of course, there might be an alternative explanation in that such behaviour would make it easier to chemically detect prey.

OTHER EVOLUTIONARY CONSIDERATIONS

Another indication that prey may face a variety of evolutionary trade-offs in defending themselves is the suggestion that antipredator tactics lack redundancy. For example, Kats, Petranka & Sih (1988) found that larvae of amphibians that have evolutionary histories of living with fish predators are often unpalatable or respond behaviourally to fish chemical cues. However, only one in four unpalatable species also responded to fish chemical cues. Of those species that were palatable, four out of five species responded to chemical cues. Similarly, Semlitsch & Gavasso (1992) found that two unpalatable species of toads (*Bufo spp.*) did not respond to chemical cues from fish or newt predators. Thus, unpalatable species apparently ignore predator chemicals (if they sense them at all) and are able to continue other fitness-enhancing activities (*e.g.*, feeding, mating).

One of the most interesting questions about predator defense mechanisms involves attempting to understand why organisms have evolved certain defensive characteristics and not others. That is, why do some organisms rely primarily on antipredator behaviours mediated via predator chemical cues while other organisms rely primarily on unpalatability or morphological adaptations? We suggest that organisms that rely on predator chemical cue detection may often have evolved chemically-mediated behavioural defenses because the chemosensory detecting abilities were already in place due to previous selection for chemical detection of food or mates. Thus, some organisms may be preadapted to detect predators via chemical cues. In addition, th reasons why some organisms respond with one set of behaviours in response to predator chemical cues while other species respond with very different behaviours are poorly understood. For example, why do some amphibian larvae respond to predator chemicals by increasing time in refuge while others respond by decreasing movement? Following the example of previous studies on amphibian larvae (Petranka, Kats & Sih, 1987; Kats, Petranka & Sih, 1988), Rodriguez & Kats (unpubl. data) examined refuge responses of Pacific treefrog tadpoles (*Hyla regilla*) to chemical cues from predatory newts. Tadpoles showed no increase in refuge use in response to predator chemical cues, but responded with a significant decrease in movement (Figure 3). If Rodriguez and Kats had only recorded refuge use they might have concluded that tadpoles do not respond to predator cues. Clearly, the behavioural assays used to measure responses to predator chemical cues should be carefully selected. Future studies should address why natural selection has favored behavioural defense in some species and palatability

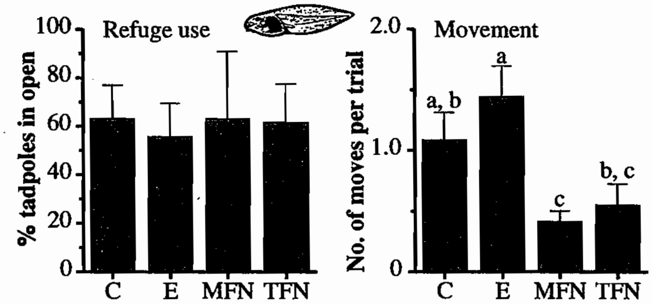

FIGURE 3. Refuge use and movement behavior af tadpoles (*Hyla regilla*) in response to tadpole skin extract and chemical cues from predatory newts (TFN = tadpole fed newts, MFN = mealworm fed newts). Shown are means and + 1 SE. Comparaisons were made using Fisher's PLSD. There was no signifiant difference for refuge use. For movement, treatments with no letters in common are significanly different from each other ($P < 0.05$). Rodriguez & Kats (unpubl. data).

defenses in others, and further, why selection favors certain behavioural defences over others (*e.g.*, reduced movement versus hiding). These studies could be approached by using phylogenetically controlled comparisons.

We also suggest that predator detection abilities might be tightly correlated with other chemosensory abilities. Individuals that are very good at chemically detecting food or mates might also be very good at detecting predators. For example, if chemosensory abilities change seasonally or if chemosensory systems are dimorphic (Dawley, 1992), primarily because of courtship and mate recognition abilities, then organisms might exhibit enhanced sensitivities to predator cues depending on chemosensory condition and receptor specificity. These experiments would be relatively easy to conduct and would help explain whether behaviours mediated via chemosensory mechanisms are positively correlated. On the other hand, Kavaliers, Wiebe and Galea (1996a,b) have suggested that there may be a negative correlation between chemically mediated behaviors. They found that when mice (*Mus musculus*) are exposed to cat odours they demonstrate a decreased interest in mate odours and an overall decrease in expression of sexually related behaviors.

SUGGESTIONS FOR FUTURE RESEARCH

As the literature on chemically mediated predator-prey interactions continues to grow we suggest a framework around which future studies could focus. Given that many experimental designs do not clearly isolate predator cues we suggest that future designs differentiate between prey responses to predator chemical cues and possible alarm substances produced by killed or injured conspecifics. Future studies might also attempt to fill in taxonomic gaps in the literature. As we pointed out earlier, there are very few studies on birds or terrestrial insects. Similarly, there are few studies on spiders (one suggests chemical detection of predators; Suter, Shane & Hirscheimer, 1989) and cartilaginous fishes. Given that most of these organisms have the physiological machinery to detect odours, we suspect that many of these species are also capable of detecting predator chemical cues. We realize that taxonomic gaps may reflect the difficulty of publishing negative results; however, we suggest that even studies that demonstrate no prey response to predator chemical cues would help explain the evolution of chemically-mediated predator detection and contribute to a better understanding of the ecological circumstances that might lead to chemically-mediated predator detection. There are few studies addressing chemically-mediated behaviours that might be correlated with one another, *i.e.*, are animals that are physiologically prepared to detect mates better or worse at detecting predators than those that lack this physiological state? Physiologists might also begin to focus on the proximate mechanisms involved in chemically mediated predator-prey interactions. For example, Heale, Vanderwolf & Kavaliers (1994) have suggested that certain parts of the brain are responsive to predator odours but do not respond to other potentially aversive odours. This suggests that certain brain regions may be involved in the elicitation of various defensive behaviours in response to predator odours. Finally, future studies should investigate complex chemical environments by examining chemically mediated predator-prey interactions in media that contain diverse chemical signals (*e.g.*, chemical signals from food sources, mates, competitors; see for example Hazlett, 1996). These types of studies might also lead to better understandings of the role of predator cue concentrations and chemical gradients. Ideally, these avenues of research could also be accompanied by a concerted effort to identify the chemical cues modulating the behaviors under consideration.

Acknowledgements

This study was support by a NSERC Canada Operating Grant (no. A6869) to L. D. and a NSF Grant (BIR-9225034) to L. K. We would like to thank the Simon Fraser University interlibrary loans staff and S. Hicks, J. Reisner, M. Kuhn, C. Vos Strache, D. Green and R. Syrdahl of Pepperdine University for logistical support. We also thank L. Dill, A. Sih, A. Blaustein, D. Chivers, J. Kiesecker, A. Fraser, J. Smith, D. Kramer, D. McQueen and M. Kavaliers for helpful suggestions on the manuscript.

Literature cited

Abbott, D. H., D. A. Baines, C. G. Faulkes, D. C. Jennens, P. C. Y. K. King & A. J. Tomlinson, 1990. A natural deer repellent: Chemistry and behaviour. Pages 599-609 *in* D. W. MacDonald, D. Müller-Schwarze & S. E. Natynczuk (ed.). Chemical Signals in Vertebrates. Oxford University Press, New York.

Alderdice, D. F., J. R. Brett, D. R. Idler & U. Fagerlund, 1954. Further observations on olfactory perception in migrating adult coho and spring salmon: Properties of the repellent in mammalian skin. Progress Report Pacific Coast Station, Fisheries Research Board Canada, 98: 10-12.

Alexander, J. E. & J. A. P. Covich, 1991. Predator avoidance by the freshwater snail *Physella virgata* in response to the crayfish *Procambarus simulans*. Oecologia, 87: 435-442.

Andelt, W. F., D. L. Baker & K. P. Burnham, 1992. Relative preference of captive cow elk for repellent treated diets. Journal of Wildlife Management, 56: 164-173.

Andelt, W. F., K. P. Burnham & J. A. Manning, 1991. Relative effectiveness of repellents for reducing mule deer damage. Journal of Wildlife Management, 55: 341-347.

Andersson, K. G., C. Brönmark, C. J. Herrmann, J. B. Malmqvist, B. C. Otto & P. Sjorstrom, 1986. Presence of sculpins (*Cottus gobio*) reduces drift and activity of *Gammarus pulex* (Amphipoda). Hydrobiologia, 133: 209-215.

Appleton, R. D. & A. R. Palmer, 1988. Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. Proceedings of the National Academy of Science, U.S.A., 85: 4387-4391.

Arnoult, C. & J. P. Signoret, 1993. Sheep food repellents: Efficacy of various products, habituation, and social facilitation. Journal of Chemical Ecology, 19: 225-236.

Audeskirk, T. & G. Audeskirk, 1985. Behavior of gastropod molluscs. Pages 1-94 *in* A. O. D. Willows (ed.). The Mollusca, Vol 8. Neurobiology and Behavior, Part 1. Academic Press, Orlando, Florida.

Ball, S. C. & R. L. Baker, 1996. Predator-induced life history changes: Antipredator behavior costs or facultative life history shifts? Ecology, 77: 1116-1124.

Barnett, C., 1982. The chemosensory responses of young cichlid fish to parents and predators. Animal Behaviour, 30: 35-42.

Barry, M. J., 1994. The costs of crest induction for *Daphnia carinata*. Oecologia, 97: 278-288.

Barry, M. J. & I. A. E. Bayly, 1985. Further studies on predator induction of crests in Australian *Daphnia* and the effects of crests on predation. Australian Journal of Marine and Freshwater Research, 36: 519-535.

Bayer, R. D., 1980. Social differences in defecation behavior of great blue herons (*Ardea herodias*). Auk, 97: 900-901.

Bengtsson, G., 1982. Energetic costs of amino acids exudation in the interaction between the predator *Gammarus pulex* L. and the prey *Asellus aquaticus*. Journal of Chemical Ecology, 8: 1271-1281.

Berg, C. J., Jr., 1972. Ontogeny of the behavior of *Strombus maculatus* (Gastropoda: Strombidae). American Zoologist, 12: 427-443.

Berg, C. J., Jr., 1974. A comparative ethological study of strombid gastropods. Behaviour, 51: 274-322.

Bertram, B. C. R., 1978. Living in groups: Predators and prey. Pages 279-309 *in* J. R. Krebs & N. B. Davies (ed.). Behavioural Ecology. Blackwell Scientific Publications, Oxford.

Black, A. R., 1993. Predator-induced phenotypic plasticity in *Daphnia pulex*: Life-history and morphological responses to *Notonecta* and *Chaoborus*. Limnology and Oceanography, 38: 986-996.

Black, A. R. & S. I. Dodson, 1990. Demographic costs of *Chaoborus*-induced phenotypic plasticity in *Daphnia pulex*. Oecologia, 83: 117-122.

Blake, M. A. & P. J. B. Hart, 1993. The behavioral responses of juvenile signal crayfish *Pacifastacus leniusculus* to stimuli from perch and eels. Freshwater Biology, 29: 89-97.

Blanchard, R. J., D. C. Blanchard, S. M. Weiss & S. Meyer, 1990. The effect of ethanol and diazepam on reactions to predatory odors. Pharmacology, Biochemistry and Behavior, 35: 775-780.

Blanchard, D. C., J. K. Shepherd, A. D. P. Carobrez & R. J. Blanchard, 1991. Sex effects in defensive behavior: Baseline differences and drug interactions. Neuroscience & Biobehavioral Reviews, 15: 461-468.

Boag, B. & J. A. Mlotkiewicz, 1994. Effects of odor derived from lion faeces on behavior of wild rabbits. Journal of Chemical Ecology, 20: 631-637.

Bogert, C. M., 1941. Sensory cues used by rattlesnakes in their recognition of Ophidian enemies. Annals of the New York Academy of Sciences, 41: 329-344.

Bollens, S. M. & B. W. Frost, 1989. Predator-induced diel vertical migration in a planktonic copepod. Journal of Plankton Research, 11: 1047-1066.

Bollens, S. M., B. W. Frost & J. R. Cordell, 1994. Chemical, mechanical and visual cues in the vertical migration of the marine planktonic copepod *Acartia hudsonica*. Journal of Plankton Research, 16: 555-564.

Boudreau, B., E. Bourget & Y. Simard 1993a. Effect of age, injury and predator odors on settlement and shelter selection by lobster *Homarus americanus* postlarvae. Marine Ecology Progress Series, 93: 119-129.

Boudreau, B., E. Bourget & Y. Simard, 1993b. Behavioural responses of competent lobster postlarvae to odor plumes. Marine Biology, 117: 63-69.

Bouskila, A., 1993. Predation risk and competition in a community of rodents and snakes. Ph.D. thesis, University of California, Davis, California.

Brett, J. R. & D. MacKinnon, 1952. Some observations on olfactory perception in migrating adult coho and spring salmon. Progress Report Pacific Coast Station, Fisheries Research Board Canada, 90: 21-23.

Brett, J. R. & D. MacKinnon, 1954. Some aspects of olfactory perception in migrating adult coho and spring salmon. Journal of the Fisheries Research Board Canada, 11: 310-318.

Bridges, C. M. & W. J. N. Gutzke, 1997. Effects of environmental history, sibship, and age on predator-avoidance responses in tadpoles. Canadian Journal of Zoology, 75: 87-93.

Brönmark, C. & J. G. Miner, 1992. Predator-induced phenotypical change in body morphology in crucian carp. Science, 258: 1348-1350.

Brönmark, C. & L. B. Petterson, 1994. Chemical cues from piscivores induce change in morphology in crucian carp. Oikos, 70: 396-402.

Brönmark, C., L. B. Petterson & P. A. Nilsson, 1993. Induced morphological defense in crucian carp: Cues, costs and benefits. Ecological Society of America Bulletin, 74: 176.

Brown, G. E. & R. J. F. Smith, 1996. Foraging trade-offs in fathead minnows (*Pimephales promelas*, Osteichthyes, Cyprinidae): Acquired predator recognition in the absence of an alarm response. Ethology, 102: 776-785.

Brown, G. E., D. P. Chivers & R. J. F. Smith, 1995a. Localized defecation by pike: A response to labelling by cyprinid alarm pheromone? Behavioral Ecology and Sociobiology, 36: 105-110.

Brown, G. E., D. P. Chivers & R. J. F. Smith, 1995b. Fathead minnows avoid conspecific and heterospecific alarm pheromones in the faeces of northern pike. Journal of Fish Biology, 47: 387-393.

Brown, G. E., D. P. Chivers & R. J. F. Smith, 1996. Effects of diet on localized defecation by northern pike, *Esox lucius*. Journal of Chemical Ecology, 22: 467-475.

Bullock, T. H., 1953. Predator recognition and escape responses of some intertidal gastropods in presence of starfish. Behaviour, 5: 130-140.

Burger, J., 1989. Following of conspecific and avoidance of predator chemical cues by pine snakes (*Pituophis melanoleucus*). Journal of Chemical Ecology, 15: 799-806.

Burger, J., 1990. Response of hatchling pine snakes (*Pituophis melanoleucus*) to chemical cues of sympatric snakes. Copeia, 1990: 1160-1163.

Burger, J., W. Boarman, L. Kurzava & M. Gochfeld, 1991. Effect of experience with pine (*Pituophis melanoleucus*) and king (*Lampropeltis getulus*) snake odors on y-maze behavior of pine snake hatchlings. Journal of Chemical Ecology, 17: 79-87.

Burke, W. R., 1964. Chemoreception by *Tegula fubebralis* (Mollusca: Gastropoda). Veliger, 6 (Suppl): 17-20.

Caine, N. G. & P. J. Weldon, 1989. Responses by red-bellied tamarins (*Saguinus labiatus*) to fecal scents of predatory and non-predatory neotropical mammals. Biotropica, 21: 186-189.

Calder, C. J. & M. L. Gorman, 1991. The effects of red fox *Vulpes vulpes* faecal odours on the feeding behaviour of Orkney voles *Microtus arvalis*. Journal of Zoology, London, 224: 599-606.

Castilla, J. C. & D. J. Crisp, 1970. Responses of *Asterias rubens* to olfactory stimuli. Journal of the Marine Biological Association of the United Kingdom, 50: 829-847.

Cattarelli, M., 1982a. Transmission and integration of biologically meaningful olfactory information after bilateral transection of the lateral olfactory tract in the rat. Behavioural Brain Research, 6: 313-337.

Cattarelli, M., 1982b. The role of the medial olfactory pathways in olfaction: Behavioral and electrophysiological data. Behavioural Brain Research, 6: 339-364.

Cattarelli, M. & J. Chanel, 1979. Influence of some biologically meaningful odorants on the vigilance states of the rat. Physiology and Behavior, 23: 831-838.

Cattarelli, M. & M. Vigouroux, 1981. Évaluation des réactions émotionelles déclenchées par des odeurs à signification biologique chez le rat au cours d'un conditionnement opérant. Physiology and Behavior, 27: 445-455.

Cattarelli, M., J. Pager & J. Chanel, 1977a. Modulation des réponses multiunitaires du bulbe olfactif et de l'activité respiratoire en fonction de la signification des odeurs chez le rat non contraint. Journal of Physiology-Paris, 73: 963-984.

Cattarelli, M., J. Pager & J. Chanel, 1977b. Modulation de l'activité du bulbe olfactif en fonction de la signification des odeurs chez le rat. Physiology and Behavior, 19: 381-387.

Cattarelli, M., E. Vernet-Maury & J. Chanel, 1974. Influences de différentes odeurs biologiques sur le comportement émotif du rat placé dans un "espace vidé d'informations". Comptes Rendus de l'Académie des Sciences Série *iii*: Sciences de la Vie-Life Sciences (Paris), 278: 2653-2656.

Chabot, D., P. Gagnon & E. A. Dixon, 1996. Effect of predator odors on heart rate and metabolic rate of wapiti (*Cervus elaphus canadensis*). Journal of Chemical Ecology, 22: 839-868.

Chesson, J., 1984. Effect of notonectids (Hemiptera: Notonectidae) on mosquitoes (Diptera: Culidicae): Predation or selective oviposition? Environmental Entomology,13: 531-538.

Chiszar, D., K. Scudder, L. Knight & H. M. Smith, 1978. Exploratory behavior in prairie rattlesnakes (*Crotalus viridis*) and water moccasins (*Agkistrodon piscivorus*). Psychological Record, 28: 363-368.

Chiszar, D., J. Perelman, H. M. Smith & D. Duvall, 1992. "Shouldering" in prairie rattlesnakes: A new hypothesis. Bulletin of the Maryland Herpetological Society, 28: 69-76.

Chivers, D. P. & R. J. F. Smith, 1993. The role of olfaction in chemosensory-based predator recognition in the fathead minnow, *Pimephales promelas*. Journal of Chemical Ecology, 19: 623-633.

Chivers, D. P. & R. J. F. Smith, 1994. The role of experience and chemical alarm signalling in predator recognition by fathead minnows, *Pimephales promelas*. Journal of Fish Biology, 44: 273-285.

Chivers, D. P., G. E. Brown & J. F. Smith, 1995a. Acquired recognition of chemical stimuli from pike, *Esox lucius*, by brook sticklebacks, *Culaea inconstans* (Osteichthyes, Gasterosteidae). Ethology, 99: 234-242.

Chivers, D. P., G. E. Brown & J. F. Smith, 1995b. Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): Implications for antipredator behaviour. Canadian Journal of Zoology, 73: 955-960.

Chivers, D. P., B. D. Wisenden & R. J. F. Smith, 1996. Damselfly larvae learn to recognize predators from chemical cues in the predator's diet. Animal Behaviour, 52: 315-320.

Clark, L., K. V. Avivola & N. J. Bean, 1993. Odor thresholds in passerines. Comparative Biochemistry and Physiology, 104A: 305-312.

Cooper, W. E., Jr., 1990. Chemical detection of predators by a lizard, the broad-headed skink (*Eumeces laticeps*). Journal of Experimental Zoology, 256: 162-167.

Cote, I. M., 1995. Effects of predatory crab effluent on byssus production in mussels. Journal of Experimental Marine Biology and Ecology, 188: 233-241.

Cott, H. B., 1940. Adaptive Coloration in Animals. Methuen, London.

Coulston, S., D. M. Stoddart & D. R. Crump, 1993. Use of predator odors to protect chick-peas from predation by laboratory and wild mice. Journal of Chemical Ecology, 19: 607-612.

Courtney, R. J., L. D. Reid, Jr. & R. E. Wasden, 1968. Suppression of running times by olfactory stimuli. Psychonomic Science, 12: 315-316.

Covich, A. P., T. A. Crowl, J. E. Alexander, Jr. & C. C. Vaughn, 1994. Predator-avoidance responses in freshwater decapod-gastropod interactions mediated by chemical stimuli. Journal of the North American Benthological Society, 13: 283-290.

Cowan, C. A. & B. L. Peckarsky, 1994. Diet feeding and positioning periodicity of a grazing mayfly in a trout stream ans a fishless stream. Canadian Journal of Fisheries and Aquatic Sciences, 51: 450-459.

Cowles, R. B., 1938. Unusual defense postures assumed by rattlesnakes. Copeia, 1938: 13-16.

Cowles, R. B. & R. L. Phelan, 1958. Olfaction in rattlesnakes. Copeia, 1958: 77-83.

Crowl, T. A. & A. P. Covich, 1990. Predator-induced life-history shifts in a freshwater snail. Science, 247: 949-951.

Crowl, T. A. & A. P. Covich, 1994. Responses of a freshwater shrimp to chemical and tactile stimuli from a large decapod predator. Journal of the North American Benthological Society, 13: 291-298.

Cupp, P. V., Jr. 1994. Salamanders avoid chemical cues from predators. Animal Behaviour, 48: 232-235.

Davy, F. B. & H. Kleerekoper, 1971. Observations on the effects of the odour of predatory fishes on the locomotor behavior of a prey (*Carassius auratus*). Texas Journal of Science, 22: 299-300.

Dawidowicz, P., 1993. Diel vertical migration in *Chaoborus flavicans*: Population patterns *versus* individual tracks. Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie, 39: 19-28.

Dawidowicz, P. & C. J. Loose, 1992. Metabolic costs during predator-induced diel vertical migration of *Daphnia*. Limnology and Oceanography, 37: 1589-1595.

Dawidowicz, P., J. Pijanowska & K. Ciechomski, 1990. Vertical migration of *Chaoborus* larvae is induced by the presence of fish. Limnology and Oceanography, 35: 1631-1637.

Dawley, E. M., 1992. Sexual dimorphism in a chemosensory system: The role of the vomeronasal organ in salamander reproductive behavior. Copeia, 1992: 113-120.

de Beauchamp, P., 1952a. Un facteur de la variabilité chez les Rotifères du genre *Brachionus*. Comptes Rendus de l'Académie des Sciences Série iii: Sciences de la Vie-Life Sciences (Paris), 234: 573-575.

de Beauchamp, P., 1952b. Variation chez les Rotifères du genre *Brachionus*. Comptes Rendus de l'Académie des Sciences Serie iii: Sciences de la Vie-Life Sciences (Paris), 235: 1355-1356.

DeMeester, L., 1993. Genotype, fish-mediated chemicals, and phototactic behavior in *Daphnia magna*. Ecology 74: 1467-1474.

Dial, B. E., 1990. Predator-prey signals: Chemosensory identification of snake predators by Eublepharid lizards and its ecological significance. Pages 555-565 *in* D. W. MacDonald, D. Müller-Schwarze & S. E. Natynczuk (ed.). Chemical Signals in Vertebrates V. Oxford University Press, New York.

Dial, B. E. & L. C. Fitzpatrick, 1981. The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). Oecologia, 51: 310-317.

Dial, B. E., P. J. Weldon & B. Curtis, 1989. Chemosensory identification of snake predators (*Phyllorhynchus decurtatus*) by banded geckos (*Coleonyx variegatus*). Journal of Herpetology, 23: 224-229.

Dickman, C. R., 1992. Predation and habitat shifts in the house mouse, *Mus domesticus*. Ecology, 73: 313-322.

Dickman, C. R. & C. P. Doncaster, 1984. Responses of small mammals to redfox (*Vulpes vulpes*) odour. Journal of Zoology, 204: 521-531.

Dieterlen, F., 1959. Das Verhalten des syrischen Goldhamsters (*Mesocricetus auratus* Waterhouse). Zeitschrift für Tierpsychologie, 16: 47-103.

Dix, T. L. & P. V. Hamilton, 1993. Chemically mediated escape behavior in the marsh periwinkle *Littoraria irrorata* Say. Journal of Experimental Marine Biology and Ecology, 166: 135-149.

Dodson, S. I., 1988a. Cyclomorphosis in *Daphnia galeata mendotae* Birge and *D. retrocurva* Forbes as a predator-induced response. Freshwater Biology, 19: 109-114.

Dodson, S. I., 1988b. The ecological role of chemical stimuli for the zooplankton: Predator-avoidance behavior in *Daphnia*. Limnology and Oceanography, 33: 1431-1439.

Dodson, S. I., 1989. The ecological role of chemical stimuli for the zooplankton: Predator-induced morphology in *Daphnia*. Oecologia, 78: 361-367.

Dodson, S. I. & J. E. Havel, 1988. Indirect prey effects: Some morphological and life history responses of *Daphnia pulex* exposed to *Notonecta undulata*. Limnology and Oceanography, 33: 1274-1285.

Dodson, S. I., T. A. Crowl, B. L. Peckarsky, L. B. Kats, A. P. Covich & J. M. Culp, 1994. Non-visual communication in freshwater benthos: An overview. Journal of the North American Benthological Society, 13: 268-282.

Douglas, P. L., G. E. Forrester & S. D. Cooper, 1994. Effects of trout on the diel periodicity of drifting in baetid mayflies. Oecologia, 98: 48-56.

Drickamer, L. C., D. G. Mikesic & K. S. Shaffer, 1992. Use of odor baits in traps to test reactions to intra- and interspecific chemical cues in house mice living in outdoor enclosures. Journal of Chemical Ecology, 18: 2223-2250.

Duval, M. A., A. M. Calzetta & D. Rittschof, 1994. Behavioral responses of *Littoraria irrorata* (Say) to water-borne odors. Journal of Chemical Ecology, 20: 3321-3334.

Edmunds, M., 1974. Defence in Animals. Longman Inc., New York.

Eisenberg, J. F. & E. Gould, 1970. The Tenrecs: A study in mammalian behavior and evolution. Smithsonian Contributions to Zoology, 27: 138 pp.

Elliott, S. A., L. B. Kats & J. A. Breeding, 1993. The use of conspecific chemical cues for cannibal avoidance in California newts (*Taricha torosa*). Ethology, 95: 186-192.

Endler, J. A., 1986. Defense against predators. Pages 109-134 *in* M. E. Feder & G. V. Lauder (ed.). Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates. University of Chicago, Chicago, Illinois.

Engelhart, A. & D. Müller-Schwarze, 1995. Responses of beaver (*Castor canadensis* Kuhl) to predator chemicals. Journal of Chemical Ecology, 21: 1349-1364.

Engelmayer, A., 1995. Effects of predator-released chemicals on some life history parameters of *Daphnia pulex*. Hydrobiologia, 307: 203-206.

Epple, G., J. R. Mason, D. L. Nolte & D. L. Campbell, 1993. Effects of predator odors on feeding in the mountain beaver (*Aplodontia rufa*). Journal of Mammalogy, 74: 715-722.

Epple, G., J. R. Mason, E. Aronov, D. L. Nolte, R. A. Hartz, R. Kaloostian, D. Campbell & A. B. Smith III, 1995. Feeding responses to predator-based repellents in the mountain beaver (*Aplodontia rufa*). Ecological Applications, 5: 1163-1170.

Fange, R., 1963. Toxic factors in starfishes. Sarsia, 10: 19-21.

Feder, H. M., 1963. Gastropod defensive responses and their effectiveness in reducing predation by starfishes. Ecology, 44: 505-512.

Feder, H. M., 1967. Organisms responsive to predatory sea stars. Sarsia, 29: 371-394.

Feder, H. M., 1972. Escape reponses in marine invertebrates. Scientific American, 227: 92-100.

Feder, H. M. & J. Arvidsson, 1967. Studies on a seastar (*Marthasterias glacialis*) extract responsible for avoidance reactions in a gastropod (*Buccinum undatum*). Arkiv För Zoology, 19: 369-379.

Feminella, J. W. & C. P. Hawkins, 1992. Predator-induced reduction in feeding by tadpoles of the tailed frog: The importance of predator chemistry. Ecological Society of America Bulletin, 73: 172.

Feminella, J. W. & C. P. Hawkins, 1994. Tailed frog tadpoles differentially alter their feeding behavior in response to non-visual cues from four predators. Journal of the North American Benthological Society, 13: 310-320.

Field, L. H., 1977. An experimental analysis of the escape response of the gastropod *Strombus maculatus*. Pacific Science, 31: 1-11.

Folt, C. & C. R. Goldman, 1981. Allelopathy between zooplankton: A mechanism for interference competition. Science, 213: 1133-1135.

Ford, L. A. & D. F. Clausen, 1941. Rodent repellent tests. Chemical and Engineering News, 19: 783.

Forward, R. B. & D. Rittschof, 1993. Activation of photoresponses of brine shrimp nauplii in diel vertical migration by chemical cues from fish. Journal of Plankton Research, 15: 693-701.

Friberg, N., T. H. Andersen, H. O. Hansen, T. M. Iverson, D. Jacobsen, L. Krojgaard & S. E. Larsen, 1994. The effect of brown trout (*Salmo trutta* L.) on stream invertebrate drift, with special reference to *Gammarus pulex* L. Hydrobiologia, 294: 105-110.

Fulk, G. W., 1972. The effects of shrews on the space utilization of voles. Journal of Mammalogy, 53: 461-478.

Geller, J. B., 1982. Chemically mediated avoidance response of a gastropod, *Tegula funebralis* (A. Adams), to a predatory crab, *Cancer antennarius* (Stimpson). Journal of Experimental Marine Biology and Ecology, 65: 19-27.

Gelowitz, C. M., A. Mathis & R. J. F. Smith, 1993. Chemosensory recognition of northern pike (*Esox lucius*) by brook stickleback (*Culaea inconstans*): Population differences and the influence of predator diet. Behaviour, 127: 105-118.

George, C. J. W., 1960. Behavioral interaction of the pickerel (*Esox niger* LeSueur and *Esox americanus* LeSueur) and the mosquitofish (*Gambusia patruelis* Baird and Girard). Ph.D. thesis, Harvard University, Cambridge, Massachusetts.

Gerlai, R., 1993. Can paradise fish (*Macropodus opercularis*, Anabantidae) recognize a natural predator? An ethological analysis. Ethology, 94: 127-136.

Gilbert, J. J., 1966. Rotifer ecology and embryological induction. Science, 151: 1234-1237.

Gilbert, J. J., 1967. *Asplanchna* and postero-lateral spine production in *Brachionus calyciflorus*. Archiv für Hydrobiologie, 64: 1-62.

Gilbert, J. J. & R. S. Stemberger, 1984. *Asplanchna*-induced polymorphism in the rotifer *Keratella slacki*. Limnology and Oceanography, 29: 1309-1316.

Gonor, J. J., 1964. Predator-prey reactions between two marine prosobranch gastropods. Veliger, 7: 228-232.

Gonor, J. J., 1966. Escape responses of North Borneo strombid gastropods elicited by the predatory prosobranchs *Aulica vespertilio* and *Conus marmoreus*. Veliger, 8: 226-230.

Gore, R. H., 1966. Observations on the escape response of *Nassarius vibex* (Say) (Mollusca: Gastropoda). Bulletin of Marine Science, 16: 423-434.

Gorman, M. L., 1984. The response of prey to stoat (*Mustela erminea*) scent . Journal of Zoology, 202: 419-423.

Gosselin, L. A., 1990. Behavioral response of *Thais emarginata* to odors of predators: Responses to fast and slow moving predators. Abstract at the Western Society of Naturalists Meeting, 1990, Monterey, California.

Goz, H., 1941. Uber den Art- und Individualgeruch bei Fischen. Zeitschrift für vergleichende Physiologie, 29: 1-45.

Grant, J. W. G. & I. A. E. Bayle, 1981. Predator induction of crests in morphs of the *Daphnia carinata* King complex. Limnology and Oceanography, 26: 201-218.

Griffith, C. R., 1920. The behavior of white rats in the presence of cats. Psychobiology, 2: 19-28.

Gutzke, W. H. N., C. Tucker & R. T. Mason, 1993. Chemical recognition of kingsnakes by crotalines: Effects of size on the ophiophage defensive response. Brain Behavior and Evolution, 41: 234-238.

Halbach, U., 1970. Die Ursachen der Temporalvariation von *Brachionus calyciflorus* Pallas (Rotatoria). Oecologia, 4: 262-318.

Hanazato, T., 1990. Induction of helmet development by a *Chaoborus* factor in *Daphnia ambigua* during juvenile stages. Journal of Plankton Research, 12: 1287-1294.

Hanazato, T., 1991a. Effects of a *Chaoborus*-released chemical on *Daphnia ambigua*: Reduction in the tolerance of the *Daphnia* to summer water temperature. Limnology and Oceanography, 36: 165-171.

Hanazato, T., 1991b. Influence of food density on the effects of a *Chaoborus*-released chemical on *Daphnia ambigua*. Freshwater Biology, 25: 477-483.

Hanazato, T., 1991c. Induction of development of high helmets by a *Chaoborus*-released chemical in *Daphnia galeata*. Archiv fur Hydrobiologie, 122: 167-175.

Hansson, L. A., 1996. Behavioural response in plants: Adjustment in algal recruitment induced by herbivores. Proceedings of the Royal Society of London (B) 263: 1241-1244.

Hara, T. J. (ed.), 1992. Fish Chemoreception. Chapman & Hall, New York.

Hart, B. L., 1990. Behavioral adaptations to pathogens and parasites: Five strategies. Neuroscience and Biobehavioral Reviews, 14: 273-294.

Harvell, C. D., 1986. The ecology and evolution of inducible defenses in a marine bryozoan: Cues, costs, and consequences. American Naturalist, 128: 810-823.

Harvell, C. D., 1990. The ecology and evolution of inducible defenses. Quarterly Review of Biology, 65: 323-340.

Harvell, C. D., 1991. Coloniality and inducible polymorphism. American Naturalist, 138: 1-14.

Harvell, C. D., 1992. Inducible defenses and allocation shifts in a marine bryozoan. Ecology, 73: 1567-1576.

Harvey, C., F. X. Garneau & J. H. Himmelman, 1987. Chemodetection by the predatory seastar *Leptasterias polaris* by the whelk *Buccinum undatum*. Marine Ecology, 40: 79-86.

Harvey, H., 1993. Predation risk and molting decisions in the Hawaiian crab *Leptodius sanguineus*: The ups and downs of an armored exoskeleton. M.Sc. Thesis, Simon Fraser University, Burnaby, British Colombia.

Havel, J. E., 1985. Cyclomorphosis of *Daphnia pulex* spined morphs. Limnology and Oceanography, 30: 853-861.

Havel, J. E., 1987. Predator-induced defenses: A review. Pages 263-278 *in* W. C. Kerfoot & A. Sih (ed.). Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover.

Hazlett, B. A., 1996. Organisation of hermit crab behaviour: Responses to multiple chemical inputs. Behaviour, 133: 619-642.

Heads, P. A., 1986. The costs of reduced feeding due to predator avoidance: Potential effects on growth and fitness in *Ischnura elegans* larvae (Odonata: Zygoptera). Ecological Entomology, 11: 369-377.

Heale, V. R. & C. H. Vanderwolf, 1994. Toluene and weasel (2-propylthietane) odors suppress feeding in the rat. Journal of Chemical Ecology, 20: 2953-2958.

Heale, V. R., C. H. Vanderwolf & M. Kavaliers, 1994. Components of weasel and fox odors elicit fast wave bursts in the dentate gyrus of rats. Behavioural Brain Research, 63: 159-165.

Hebert, P. D. N. & P. M. Grewe, 1985. *Chaoborus*-induced shifts in the morphology of *Daphnia ambigua*. Limnology and Oceanography, 30: 1291-1297.

Heikkila, J., L. Kaarsalo, O. Mustonen & P. Pekkarinen, 1993. Influence of predation risk on early development and maturation in three species of *Clethrionomys* voles. Annalles Zoological Fennici, 30: 153-161.

Hennessy, D. F. & D. H. Owings, 1978. Snake species discrimination and the role of olfactory cues in the snake-directed behavior of the California ground squirrel. Behaviour, 65: 115-124.

Hoffman, D. L. & P. J. Weldon, 1978. Flight reponses of two intertidal gastropods (Prosobranchia: Trochidae) to sympatric predatory gastropods from Barbados. Veliger, 20: 361-366.

Holomuzki, J. R., 1995. Oviposition sites and fish-deterrent mechanisms in two stream anurans. Copeia, 1995: 607-613.

Holomuzki, J. R. & L. A. Hatchett, 1994. Predator avoidance costs and habituation to fish chemicals by a stream isopod. Freshwater Biology, 32: 585-592.

Holomuzki, J. R. & J. D. Hoyle, 1990. Effect of predatory fish presence on habitat use and diel movement of the stream amphipod, *Gammarus minus*. Freshwater Biology, 24: 509-517.

Holomuzki, J. R. & T. M. Short, 1988. Habitat use and fish avoidance behaviors by the stream-dwelling isopod *Lirceus fontinalis*. Oikos, 52: 79-86.

Holomuzki, J. R. & T. M. Short, 1990. Ontogenetic shifts in habitat use and activity in a stream-dwelling isopod. Holarctic Ecology, 13: 300-307.

Horat, P. & R. D. Semlitsch, 1994. Effects of predation risk and hunger on the behaviour of two species of tadpoles. Behavioral Ecology and Sociobiology, 34: 393-401.

Howard, R. W., D. W. Stanley-Samuelson & R. D. Akre, 1990. Biosynthesis and chemical mimicry of cuticular hydrocarbons from the obligate predator, *Microdon albicomatus* Novak (Diptera: Syrphidae) and its ant prey, *Myrmica incompleta* Provancher (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society, 63: 437-443.

Howe, N. R. & L. G. Harris, 1978. Transfer of the sea anemone pheromone, anthopleurine, by the nudibranch *Aeolidia papillosa*. Journal of Chemical Ecology,4: 551-561.

Idler, J. R., U. H. M. Fagerlund & H. Mayoh, 1956. Olfactory perception in migrating salmon. I. L-serine, a salmon repellent in mammalian skin. Journal of General Physiology, 39: 889-892.

Iwasaki, K., 1993. Analyses of limpet defense and predator offense in the field. Marine Biology, 116: 277-289.

Jachner, A., 1995a. Chemically-induced habit shifts in bleak (*Alburnus alburnus* L.). Archiv für Hydrobiologie, 133: 71-79.

Jachner, A., 1995b. Changes in feeding behavior of bleak (*Alburnus alburnus*) in response to visual and chemical stimuli from predators. Archiv fur Hydrobiologie, 133: 305-314.

Jackson, J. F., 1990. Evidence for chemosensor-mediated predator avoidance in musk turtles. Copeia, 1990: 557-560.

Jackson, M. E. & R. D. Semlitsch, 1993. Paedomorphosis in the salamander *Ambystoma talpoideum*: Effects of a fish predator. Ecology, 74: 342-350.

Jaiswal, S. K. & S. Waghray, 1990. Quantification of defence reactions of cichlid fish, *Oreochromis mossambicus* (Peters) Trewavas, in response to warning chemicals. Indian Journal of Animal Sciences, 60: 1137-1145.

Jedrzejewski, W. & B. Jedrzejewska, 1990. Effect of a predator's visit on the spatial distribution of bank voles: Experiments with weasels. Canadian Journal of Zoology, 68: 660-666.

Jedrzejewski, W., L. Rychlik & B. Jedrzejewska, 1993. Responses of bank voles to odours of seven species of predators: Experimental data and their relevance to natural predator-vole relationships. Oikos, 68: 251-257.

Jerka-Dziadosz, M., C. Dosche, H. W. Kuhlmann & K. Heckmann, 1987. Signal-induced reorganization of the microtubular cytoskeleton in the ciliated protozoon *Euplotes octocarinatus*. Journal of Cell Science, 87: 555-564.

Johnson, L. E. & R. R. Strathmann, 1989. Settling barnacle larvae avoid substrata previously occupied by a mobile predator. Journal of Experimental Marine Biology and Ecology, 128: 87-103.

Kare, M. R. & J. R. Mason, 1986. The chemical senses in birds. Pages 59-67 *in* P. D. Sturkie (ed.). Avian Physiology, 4th ed. Springer-Verlag, New York.

Kasumyan, A. O. & N. I. Pashchenko, 1985. Olfactory way of alarm kairomone perception by fishes. Vestnik Moskovskii Universitet Biologiya, 40: 50-54.

Kats, L. B., 1988. The detection of certain predators via olfaction by small-mouthed salamander larvae (*Ambystoma texanum*). Behavioral Neural Biology, 50: 126-131.

Kats, L. B. & A. Sih, 1992. Oviposition site selection and avoidance of fish by streamside salamanders (*Ambystoma barbouri*). Copeia, 1992: 468-473.

Kats, L. B., J. W. Petranka & A. Sih, 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. Ecology, 69: 1865-1870.

Kats, L. B., J. A. Breeding, K. M. Hanson & P. Smith, 1994. Ontogenetic changes in California newts (*Taricha torosa*) in response to chemical cues from conspecific predators. Journal of the North American Benthological Society, 13: 321-325.

Kavaliers, M., 1988. Brief exposure to a natural predator, the short-tailed weasel, induces benzodiazepine-sensitive analgesia in white footed mice. Physiology and Behavior, 43: 187-193.

Kavaliers, M., 1990. Responsiveness of deer mice to a predator, the short-tailed weasel: Population differences and neuromodulatory mechanisms. Physiological Zoology, 63: 388-407.

Kavaliers, M. & D. D. Colwell, 1995. Decreased predator avoidance in parasitized mice: Neuromodulatory correlates. Parasitology, 111: 257-263.

Kavaliers, M. & D. D. Colwell, 1996. Synergism between stress responses induced by biting flies and predator odours. Ethology, 102: 89-98.

Kavaliers, M., J. P. Wiebe & L. A. M. Galea, 1994a. Reduction of predator odor-induced anxiety in mice by the neurosteroid 3(-hydroxy-4-pregnen-20-one (3(HP). Brain Research, 645: 325-329.

Kavaliers, M., J. P. Wiebe & L. A. M. Galea, 1994b. Male preference for the odors of estrous female mice is enhanced by the neurosteroid 3(-hydroxy-4-pregnen-20-one (3(HP). Brain Research, 646: 140-144.

Kaveliers, M., D. Innes & K. P. Ossenkopp, 1991. Predator-odor analgesia in deer mice: Neuromodulatory mechanisms and sex differences. Pages 529-535 *in* R. L. Doty & D. Müller-Schwarze (ed.). Chemical Signals in Vertebrates VI. Plenum Press, New York.

Keefe, M. L., 1992. Chemically mediated avoidance behavior in wild brook trout, *Salvelinus fontinalis*: The response to familiar and unfamiliar predaceous fishes and the influence of fish diet. Canadian Journal of Zoology, 70: 288-292.

Keefe, M. L., T. A. Whitesel & H. E. Winn, 1991. Learned predator avoidance behavior and a two-level system for chemosensory recognition of predatory fishes in juvenile brook trout. Pages 375-382 *in* R. L. Doty & D. Müller-Schwarze (ed.). Chemical Signals in Vertebrates VI. Plenum Press, New York.

Kerfoot, W. C., 1987. Translocation experiments: *Bosmina* responses to copepod predation. Ecology, 68: 596-610.

Kiesecker, J. M., D. P. Chivers & A. R. Blaustein, 1996. The use of chemical cues in predator recognition by western toad tadpoles. Animal Behaviour, 52: 1237-1245.

Knapp, R. A., 1993. The influence of egg survivorship on the subsequent nest fidelity of female bicolor damselfish, *Stegastes partitus*. Animal Behaviour, 46: 111-121.

Kohler, S. L. & M. A. McPeek, 1989. Predation risk and the foraging behavior of competing stream insects. Ecology, 70: 1811-1825.

Kohn, A. J., 1961. Chemoreception in gastropod molluscs. American Zoologist, 1: 291-308.

Koskela, E. & H. Ylönen, 1995. Suppressed feeding in the field vole (*Microtus agrestis*): An adaptation to cyclically fluctuating predation risk. Behavioral Ecology, 6: 311-315.

Kraus, F. & J. W. Petranka, 1989. A new sibling species of *Ambystoma* from the Ohio river drainage. Copeia, 1989: 94-110.

Krueger, D. A. & S. I. Dodson, 1981. Embryological induction and predation ecology in *Daphnia pulex*. Limnology and Oceanography, 26: 219-223.

Kuhlmann, H. W. & K. Heckmann, 1985. Interspecific morphogens regulating prey-predator relationships in protozoa. Science, 227: 1347-1349.

Kusch, J., 1993a. Induction of defensive morphological changes in ciliates. Oecologia, 94: 571-575.

Kusch, J., 1993b. Predator-induced morphological changes in *Euplotes* (Ciliata): Isolation of the inducing substance released from *Stenostomum shagnetorum* (Turbellaria). Journal of Experimental Zoology, 265: 613-618.

Kusch, J., 1993c. Behavioural and morphological changes in ciliates induced by the predator *Amoeba proteus*. Oecologia, 96: 354-359.

Kusch, J. & K. Heckmann, 1992. Isolation of the *Lembadion*-factor, a morphogenetically active signal, that induces *Euplotes* cells to change from their ovoid form into a larger lateral winged morph. Developmental Genetics, 13: 241-246.

Kusch, J. & H. W. Kuhlmann, 1994. Cost of *Stenostomum*-induced morphological defence in the ciliate *Euplotes octocarinatus*. Archiv für Hydrobiologie, 130: 257-267.

Kvam, O. V., 1993. Effects of chemical signals in a system with zooplankton and invertebrate predators (in Norwegian). M.Sc. Thesis, University of Bergen, Bergen.

Kvam, O. V. & O. T. Kleiven, 1995. Diel horizontal migration and swarm formation in *Daphnia* in response to *Chaoborus*. Hydrobiologia, 307: 177-184.

Lauridsen, T. L. & D. M. Dodge, 1996. Avoidance by *Daphnia magna* of fish and macrophytes: Chemical cues and predator-mediated use of macrophyte habitat. Limnology and Oceanography, 41: 794-798.

Lefcort, H., 1996. Adaptive, chemically mediated fright response in tadpoles of the southern leopard frog, *Rana utricularia*. Copeia, 1996: 455-459.

Lefcort, H. & S. M. Eiger, 1993. Antipredatory behaviour of feverish tadpoles: Implications for pathogen transmisssion. Behaviour, 126: 13-27.

Leguault, C. & J. H. Himmelman, 1993. Relation between escape behaviour of benthic marine invertebrates and the risk of predation. Journal of Experimental Marine Biology and Ecology, 170: 55-74.

Lima, S. L. & L. M. Dill, 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology, 68: 619-640.

Lively, C. M., 1986. Predator-induced shell dimorphism in the acorn barnacle, *Chthamalus anisopoma*. Evolution, 40: 232-242.

Loose, C. J., 1993a. Lack of endogenous rhythmicity in *Daphnia* diel vertical migration. Limnology and Oceanography, 38: 1837-1841.

Loose, C. J., 1993b. *Daphnia* diel vertical migration behavior: Response to vertebrate predator abundance. Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie, 39: 29-36.

Loose, C. J. & P. Dawidowicz, 1994. Trade-offs in vertical migration by zooplankton: The costs of predator avoidance. Ecology, 75: 2255-2263.

Loose, C. J., E. Von Ellert & P. Dawidowicz, 1993. Chemically-induced diel vertical migration in *Daphnia*: A new bioassay for kairomones exuded by fish. Archiv für Hydrobiologie, 126: 329-337.

Lüning, J., 1992. Phenotypic plasticity of *Daphnia pulex* in the presence of invertebrate predators: Morphological and life history responses. Oecologia, 92: 383-390.

Lüning, J., 1994. Anti-predator defenses in *Daphnia*- are life-history changes always linked to induced neck spines? Oikos, 69: 427-436.

Lyons, D. M. & E. M. Banks, 1982. Ultrasounds in neonatal rats: Novel, predator and conspecific odor cues. Developmental Psychobiology, 15: 455-460.

Macchiusi, F. & R. L. Baker, 1992. Effects of predators and food availability on activity and growth of *Chironomus tentans* (Chironomidae: Diptera). Freshwater Biology, 28: 207-216.

MacGinitie, G. E. & N. MacGinitie, 1968. Natural History of Marine Animals, 2nd ed. McGraw-Hill, Toronto, Ontario.

Máchacek, J., 1991. Indirect effect of planktivorous fish on the growth and reproduction of *Daphnia galeata*. Hydrobiologia, 225: 193-197.

Máchacek, J., 1993. Comparison of the response of *Daphnia galeata* and *Daphnia obtusa* to fish-produced chemical substance. Limnology and Oceanography, 38: 1544-1550.

Mackie, A. M., 1970a. The escape reactions of marine invertebrates to predatory starfish. Pages 269-274 *in* B. Battaglia (ed.). Fifth European Marine Biology Symposium, Padova.

Mackie, A. M., 1970b. Avoidance reactions of marine invertebrates to either steroid glycosides of starfish or synthetic surface-active agents. Journal of Experimental Marine Biology and Ecology, 5: 63-69.

Mackie, A. M. & P. T. Grant, 1974. Interspecies and intraspecies chemoreception by marine invertebrates. Pages 105-141 *in* P. T. Grant & A. M. Mackie (ed.). Chemoreception in Marine Organisms. Academic Press, New York.

Mackie, A. M., R. Lasker & P. T. Grant, 1968. Avoidance reactions of a mollusc *Buccinum undatum* to saponin-like surface-active substances in extracts of the starfish *Asterias rubens* and *Marthasterias glacialis*. Comparative Biochemistry and Physiology, 26: 415-428.

Magurran, A. E., 1989. Acquired recognition of predator odour in the European minnow (*Phoxinus phoxinus*). Ethology, 82: 216-223.

Magurran, A. E. & A. Higham, 1988. Information transfer across fish shoals under predator threat. Ethology, 78: 153-158.

Malmqvist, B., 1992. Stream grazer responses to predator odour: An experimental study. Nordic Journal of Freshwater Research, 67: 27-34.

Malyushina, G. A., A. O. Kasumyan & E. A. Marusov, 1991. Ecological aspects of chemical signals in fish. Journal of Ichthyology, 31: 1-7.

Mann, K. H., J. L. C. Wright, B. E. Welsford & E. Hatfield, 1984. Responses of the sea urchin *Strongylocentrotus droebachiensis* (O. F. Muller) to water-borne stimuli from potential predators and potential food algae. Journal of Experimental Marine Biology and Ecology, 79: 233-244.

Manteifel, Y., 1995. Chemically-mediated avoidance of predators by *Rana temporaria* tadpoles. Journal of Herpetology, 29: 461-463.

Mappes, T. & H. Ylönen, 1992. Predation risk and population density effects on the breeding tactics of the bank vole. Abstract International Society Behavioral Ecology, Princeton, New Jersey.

Marchisin, A., 1980. Predator-prey interactions between snake-eating snakes and pit vipers. Ph.D. Thesis, Rutgers University.

Margolin, A. S., 1964. The mantle response of *Diodora aspera*. Animal Behaviour, 12: 187-194.

Marinone, M. C. & H. E. Zagarese, 1991. A field and laboratory study on factors affecting polymorphism in the rotifer *Keratella tropica*. Oecologia, 86: 372-377.

Marko, P. B. & A. R. Palmer, 1991. Responses of a rocky shore gastropod to the effluents of predatory and non-predatory crabs: Avoidance and attraction. Biological Bulletin, 181: 363-370.

Martel, G. , 1996. Growth rate and influence of predation risk on territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of fisheries and Aquatic Sciences, 53: 660-669.

Martel, G. & L. M. Dill, 1993. Feeding and aggressive behaviours in juvenile coho salmon (*Oncorhynchus kisutch*) under chemically-mediated risk of predation. Behavioral Ecology and Sociobiology, 32: 365-370.

Martinez, L. A., 1987. Sensory mechanisms underlying the predator-prey interaction between perlodid stonefly nymphs and their mayfly prey. Ph.D. Thesis, Cornell University, Ithaca, New York.

Martinez, L. A. & B. L. Peckarsky, 1993. The use of non-visual cues by stream-dwelling invertebrates. Bulletin of the North American Benthological Society, 10: 103.

Mason, J. R., L. Clark & P. S. Shah, 1991. Ortho-aminoacetophenone repellency to birds: Similarities to methyl anthranilate. Journal of Wildlife Management, 55: 334-340.

Mason, J. R., G. Epple & D. L. Nolte, 1994. Semiochemicals and improvements in rodent control. Pages 327-346 *in* B. G. Galef, Jr, M. Mainardi & P. Valsecchi (ed.). Behavioral Aspects of Feeding. Harwood Academic Publication, Chur.

Mathis, A. & R. J. F. Smith, 1993a. Fathead minnows, *Pimephales promelas*, learn to recognize northern pike, *Esox lucius*, as predators on the basis of chemical stimuli from minnows in the pike's diet. Animal Behaviour, 46: 645-656.

Mathis, A. & R. J. F. Smith, 1993b. Chemical labeling of northern pike (*Esox lucius*) by the alarm pheromone of fathead minnows (*Pimephales promelas*). Journal of Chemical Ecology, 19: 1967-1979.

Mathis, A., D. P. Chivers & R. J. F. Smith, 1993. Population differences in responses of fathead minnows (*Pimephales promelas*) to visual and chemical stimuli from predators. Ethology, 93: 31-40.

Mathis, A., D. P. Chivers & R. J. F. Smith, 1996. Cultural transmission of predator recognition in fishes: Intraspecific and interspecific learning. Animal Behaviour, 51: 185-201.

Matity, J. G., D. P. Chivers & R. J. F. Smith, 1994. Population and sex differences in antipredator responses of breeding fathead minnows (*Pimephales promelas*) to chemical stimuli from garter snakes (*Thamnophis radix* and *T. sirtalis*). Journal of Chemical Ecology, 20: 2111-2121.

McIntosh, A. R. & B. L. Peckarsky, 1996. Differential behavioral responses of mayflies from streams with and without fish to trout odour. Freshwater Biology, 35: 141-148.

McKelvey, L. M. & R. B. Forward, Jr., 1995. Activation of brine shrimp nauplii photoresponses involved in diel vertical migration by chemical cues from visual and non-visual planktivores. Journal of Plankton Research, 17: 2191-2206.

McKillup, S. C., 1981. Avoidance of the predatory whelk *Lepsiella scobina albomarginata* by *Littorina cincta* and *Littorina unifasciata*. Veliger, 24: 167-171.

McKillup, S. C. & R. V. McKillup, 1993. Behavior of the intertidal gastropod *Planaxis sulcatus* (Cerithiacea: Planaxidae) in Fiji: Are responses to damaged conspecifics and predators more pronounced on tropical *versus* temperate shores? Pacific Science, 47: 401-407.

Melchiors, M. A. & C. A. Leslie, 1985. Effectiveness of predator fecal odors as black-tailed deer repellents. Journal of Wildlife Management, 49: 358-362.

Merkens, M., A. S. Harestad & T. P. Sullivan, 1991. Cover and efficacy of predator-based repellents for Townsend's vole, *Microtus townsendii*. Journal of Chemical Ecology, 17: 401-412.

Montague, T. L., D. C. Pollock & W. Wright, 1990. An examination of the browsing animal problem in Australian eucalypt and pine plantations. Proceedings of the Vertebrate Pest Conferences, 14: 203-208.

Montgomery, D. H., 1967. Responses of two haliotid gastropods (Mollusca), *Haliotis assimilis* and *Haliotis rufescens*, to the forcipulate asteroids (Echinodermata), *Pycnopodia helianthoides* and *Pisaster ochraceus*. Veliger, 9: 359-368.

Moore, R. D., B. Newton & A. Sih, 1996. Delayed hatching as a response of streamside salamander eggs to chemical cues from predatory sunfish. Oikos, 77: 331-335.

Moyle, P. B. & J. J. Cech, Jr., 1988. Fishes: An Introduction to Ichthyology. Prentice Hall, Englewood Cliffs, New Jersey.

Müller-Schwarze, D., 1972. Responses of young black-tailed deer to predator odors. Journal of Mammalogy, 53: 393-394.

Müller-Schwarze, D., 1983. Experimental modulation of behavior of free-ranging mammals by semiochemicals. Pages 235-244 *in* D. Müller-Schwarze & R. M. Silverstein (ed.). Chemical Signals in Vertebrates III. Plenum Press, New York.

Neill, W. E., 1990. Induced vertical migration in copepods as a defence against invertebrate predation. Nature, 345: 524-526.

Nisbet, I. C. T., 1983. Defecation behavior of territorial and nonterritorial common terns (*Sterna hirundo*). Auk, 100: 1001-1002.

Nolte, D. L., J. P. Farley, D. L. Campbell, G. Epple & J. R. Mason, 1993. Potential repellents to prevent mountain beaver damage. Pesticide Science, 12: 624-626.

Nolte, D. L., J. R. Mason, G. Epple, E. Aranov & D. L. Campbell, 1994. Why are predator urines aversive to prey? Journal of Chemical Ecology, 20: 1505-1516.

Novellie, P., R. C. Bigalke & D. Pepler, 1982. Can predator urine be used as a buck or rodent repellent? Suid-Afr. Bosboutydskrif, 123: 51-55.

Ode, P. R. & S. A. Wissinger, 1993. Interaction between chemical and tactile cues in mayfly detection of stoneflies. Freshwater Biology, 30: 351-357.

Ostermeyer, M. C. & R. W. Elwood, 1983. Pup recognition in *Mus musculus*: Parental discrimination between own and alien young. Developmental Psychobiology, 16: 75-82.

Palmer, A. R., 1981. Do carbonate skeletons limit the rate of body growth? Nature, 292: 150-152.

Palmer, A. R., 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). Hydrobiologia, 193: 155-182.

Parejko, K., 1991. Predation by chaoborids on typical and spined *Daphnia pulex*. Freshwater Biology, 25: 211-217.

Parejko, K. & S. Dodson, 1990. Progress towards characterization of a predator/prey kairomone: *Daphnia pulex* and *Chaoborus americanus*. Hydrobiologia, 198: 51-59.

Parejko, K. & S. Dodson, 1991. The evolutionary ecology of an antipredator reaction norm: *Daphnia pulex* and *Chaoborus americanus*. Evolution, 45: 1665-1674.

Parsons, G. J. & S. Bondrup-Nielsen, 1996. Experimental analysis of behaviour of meadow voles (*Microtus pennsylvanicus*) to odours of the short-tailed weasel (*Mustela erminea*). Écoscience, 3: 63-69.

Peckarsky, B. L., 1980. Predator-prey interactions between stoneflies and mayflies: Behavioral observations. Ecology, 61: 932-943.

Peckarsky, B. L. & S. I. Dodson, 1980. Do stonefly predators influence benthic distributions in streams? Ecology, 61: 1275-1282.

Peters, R. S., 1964. Function of the cephalic tentacles in *Littorina planaxis* Philippi (Gastropoda: Prosobranchia). Veliger, 7: 143-148.

Perrot-Sinal, T. S., V. R. Heale, K. P. Ossenkopp & M. Kavaliers, 1996. Sexually dimorphic aspects of spontaneous activity in meadow voles (*Microtus pennsylvanicus*): Effects of exposure to fox odor. Behavioral Neuroscience, 110: 1126-1132.

Petranka, J. W. & K. Fakhoury, 1991. Evidence of a chemically-mediated avoidance response of ovipositing insects to bluegills and green frog tadpoles. Copeia, 1991: 234-239.

Petranka, J. W., L. B. Kats & A. Sih, 1987. Predator-prey interactions among fish and larval amphibians: Use of chemical cues to detect predatory fish. Animal Behaviour, 35: 420-425.

Pfister, J. A., D. Müller-Schwarze & D. F. Balph, 1990. Effects of predator fecal odors on feed selection by sheep and cattle. Journal of Chemical Ecology, 16: 573-583.

Phillips, D. W., 1975a. Distance-chemoreception triggered avoidance behavior of the limpets *Acmaea* (*Collisella*) *limatula* and *Acmaea* (*Notoacmea*) *scutum* to the predatory starfish *Pisaster ochraceus*. Journal of Experimental Zoology, 191: 199-210.

Phillips, D. W., 1975b. Localization and electrical activity of the distance chemoreceptors that mediate predator avoidance behaviour in *Acmaea limatula* and *Acmaea scutum* (Gastropoda, Prosobranchia). Journal of Experimental Biology, 63: 403-412.

Phillips, D. W., 1976. The effect of a species-specific avoidance reponse to predatory starfish on the intertidal distribution of two gastropods. Oecologia, 23: 83-94.

Phillips, D. W., 1977. Avoidance and escape responses of the gastropod mollusc *Olivella biplicata* (Sowerby) to predatory asteroids. Journal of Experimental Marine Biology and Ecology, 28: 77-86.

Phillips, D. W., 1978. Chemical mediation of invertebrate defensive behaviors and the ability to distinguish between foraging and inactive predators. Marine Biology, 49: 237-243.

Phillips, J. A. & A. C. Alberts, 1992. Naive ophiophagus lizards recognize and avoid venomous snakes using chemical cues. Journal of Chemical Ecology, 18: 1775-1783.

Pitcher, T. J., 1986. Functions of shoaling behaviour in teleosts. Pages 294-337 *in* T. J. Pitcher (ed.). The Behaviour of Teleost Fishes. Croom Helm, London.

Pitcher, T. J., S. H. Lang & J. A. Turner, 1988. A risk-balancing trade-off between foraging rewards and predation hazard in a shoaling fish. Behavioral Ecology and Sociobiology, 22: 225-228.

Pourriot, R., 1974. Relations prédateur-proie chez les rotifères: Influence du prédateur (*Asplanchna brightwelli*) sur la morphologie de la proie (*Brachionus bidentata*). Annales d'Hydrobiologie, 5: 43-55.

Ramcharan, C. W., S. I. Dodson & J. Lee, 1992. Predation risk, prey behavior, and feeding rate in *Daphnia pulex*. Canadian Journal of Fisheries and Aquatic Sciences, 49: 159-165.

Randall, J. A. & C. M. Stevens, 1987. Footdrumming and other anti-predator responses in the bannertail kangaroo rat (*Dipodomys spectabilis*). Behavioral Ecology and Sociobiology, 20: 187-194.

Randall, J. A., S. M. Hatch & E. R. Hekkala, 1995. Inter-specific variation in anti-predator behavior in sympatric species of kangaroo rat. Behavioral Ecology and Sociobiology, 36: 243-250.

Recher, H. F. & J. A. Recher, 1972. Herons leaving the water to defecate. Auk, 89: 896-897.

Reed, J. R., 1969. Alarm substances and fright reaction in some fishes from the southeastern United States. Transaction of the American Fisheries Society, 98: 664-668.

Reede, T. & J. Ringleberg, 1995. The influence of a fish exudate on two clones of the hybrid *Daphnia galeata x hyalina*. Hydrobiologia, 307: 207-212.

Rehnberg, B. G. & C. B. Schreck, 1987. Chemosensory detection of predators by coho salmon (*Oncorhynchus kisutch*): Behavioral reaction and the physiological stress response. Canadian Journal of Zoology, 65: 481-485.

Rehnberg, B. G., B. Jonasson & C. B. Schreck, 1985. Olfactory sensitivity during parr and smolt developmental stages of coho salmon. Transaction of the American Fisheries Society, 114: 732-736.

Reiff, M., 1956. Untersuchungen uber naturliche und synthetische Geruchstoffe, die bei Ratten und Mausen eine stimulierende Wirkung auslosen. Acta Tropica, 13: 289-318.

Repka, S., M. Ketola & M. Walls, 1994. Specificity of predator-induced neck spine and alteration in life history traits in *Daphnia pulex*. Hydrobiologia, 294: 129-140.

Resetarits, W. J., Jr. & H. M. Wilbur, 1989. Choice of oviposition site by *Hyla chrysoscelis*: Role of predators and competitors. Ecology, 70: 220-228.

Richardson, W. B., 1942. Reaction toward snakes as shown by the wood rat, *Neotoma albigula*. Journal of Comparative Psychology, 34: 1-10.

Ringelberg, J., 1991a. Enhancement of the phototactic reaction in *Daphnia hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). Journal of Plankton Research, 13: 17-25.

Ringelberg, J., 1991b. A mechanism of predator-mediated induction of diel vertical migration in *Daphnia hyalina*. Journal of Plankton Research, 13: 83-89.

Ringelberg, J., 1991c. The relation between ultimate and proximate aspects of diel vertical migration in *Daphnia hyalina*. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnology, 24: 2804-2807.

Robertson, R., 1961. The feeding of *Strombus* and related herbivorous marine gastropods. Notulae Naturae, 343: 1-9.

Robinson, I., 1990. The effect of mink odour on rabbits and small mammals. Pages 566-572 *in* D. W. MacDonald (ed.). Chemical Signals in Vertebrates V. Oxford University Press, New York.

Roca, J. R. & D. L. Danielopol, 1996. Exploration of interstitial habitats by the phytophilous Ostracod *Cyridopsis vidua* (O.F. Muller): Experimental evidence. Annals of Limnology, 27: 243-252.

Roca, J. R., A. Baltanas & F. Uiblein, 1993. Adaptive responses in *Cypridopsis vidua* (Crustacea: Ostracoda) to food and shelter offered by a macrophyte (*Chara fragilis*). Hydrobiologia, 262: 127-131.

Ronkainen, H. & H. Ylonen, 1994. Behaviour of cyclic bank voles under risk of mustelid predation: Do females avoid copulations? Oecologia, 97: 377-381.

Roudebush, R. E. & D. H. Taylor, 1987. Chemical communication between two species of desmognathine salamanders. Copeia, 1987: 744-748.

Rowland, W. J., C. C. Robb & S. A. Cortwright, 1990. Chemically-mediated mate choice in red-spotted newts: Do males select or just detect females? Animal Behaviour, 39: 811-813.

Schaller, G. B., 1972. The Serengeti Lion: A Study of Predator-Prey Relations. University of Chicago Press, Chicago, Illinois.

Scheibling, R. E. & J. Hamm, 1991. Interactions between sea urchins (*Strongylocentrotus droebachiensis*) and their predators in field and laboratory experiments. Marine Biology, 110: 105-116.

Schwartz, S. S., 1991. Predator-induced alterations in *Daphnia* morphology. Journal of Plankton Research, 13: 1151-1161.

Scrimgeour, G. J., J. M. Culp & K. J. Cash, 1994. Anti-predator responses of mayfly larvae to conspecific and predator stimuli. Journal of the North American Benthological Society, 13: 299-309.

Semlitsch, R. D. & S. Gavasso, 1992. Behavioral responses of *Bufo bufo* and *Bufo calamita* tadpoles to chemical cues of vertebrate and invertebrate predators. Ethology, Ecology and Evolution, 4: 1-9.

Shave, C. R., C. R. Townsend & T. A. Crowl, 1994. Anti-predator behaviours of a freshwater crayfish (*Paranephrops zealandicus* White) to a native and an introduced predator. New Zealand Journal of Ecology, 18: 1-10.

Short, T. M. & J. R. Holomuzki, 1992. Indirect effects of fish on foraging behaviour and leaf processing by the isopod *Lirceus fontinalis*. Freshwater Biology, 27: 91-97.

Sih, A., 1986. Antipredator responses and the perception of danger by mosquito larvae. Ecology, 67: 434-441.

Sih, A. & L. B. Kats, 1991. Effects of refuge availability on the responses of salamander larvae to chemical cues from predatory green sunfish. Animal Behaviour, 42: 330-332.

Sih, A. & L. B. Kats, 1994. Age, experience, and the response of streamside salamander hatchlings to chemical cues from predatory sunfish. Ethology, 96: 253-259.

Sih, A. & R. D. Moore, 1993. Delayed hatching of salamander eggs in response to enhanced larval predation risk. American Naturalist, 142: 947-960.

Sih, A., L. B. Kats & R. D. Moore, 1992. Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. Ecology, 73: 1418-1430.

Skelly, D. K., 1992. Field evidence for a cost of behavioral antipredator response in a larval amphibian. Ecology, 73: 704-708.

Smith, R. J. F., 1989. The response of *Asterropteryx semipunctatus* and *Gnatholepis anjerensis* (Pisces, Gobiidae) to chemical stimuli from injured conspecifics, an alarm response in gobies. Ethology, 81: 279-290.

Snyder, N. F. R., 1967. An alarm reaction of aquatic gastropods to intraspecific extract. Cornell University Agriculture Experimental Station, Memoir, 403: 1-122.

Snyder, N. F. R. & H. A. Snyder, 1971. Pheromone-mediated behaviour of *Fasciolaria tulipa*. Animal Behaviour, 19: 257-268.

Soluk, D. A., 1990. Postmolt susceptibility of *Ephmerella* larvae to predatory stoneflies: Constraints on defensive armour. Oikos, 58: 336-342.

Spitze, K., 1992. Predator-mediated plasticity of prey life-history and morphology: *Chaoborus americanus* predation on *Daphnia pulex*. American Naturalist, 139: 229-247.

Stauffer, H. P. & R. D. Semlitsch, 1993. Effects of visual, chemical and tactile cues of fish on the behavioural responses of tadpoles. Animal Behaviour, 46: 355-364.

Stemberger, R. S., 1990. Food limitation, spination, and reproduction in *Branchionus calyciflorus*. Limnology and Oceanography, 35: 33-44.

Stemberger, R. S. & J. J. Gilbert, 1984. Spine development in the rotifer *Keratella cochlearis*: induction by cyclopoid copepods and *Asplanchna*. Freshwater Biology, 14: 639-647.

Stemberger, R. S. & J. J. Gilbert, 1987. Multiple-species induction of morphological defenses in the rotifer *Keratella testudo*. Ecology, 68: 370-378.

Stenson, J. A. E., 1987. Variation in capsule size of *Holopedium gibberum* (Zaddach): A response to invertebrate predation. Ecology, 68: 928-934.

Stenson, J. A. E., 1988. Predator-induced defense in *Holopedium gibberum* (Zaddach). Bulletin of Marine Science, 43: 850.

Stibor, H., 1992. Predator induced life-history shifts in a freshwater cladoceran. Oecologia, 92: 162-165.

Stibor, H. & J. Lüning, 1994. Predator-induced phenotypic variation in the pattern of growth and reproduction in *Daphnia hyalina* (Crustacea: Cladocera). Functional Ecology, 8: 97-101.

Stirling, G., 1995. *Daphnia* behaviour as a bioassay of fish presence or predation. Functional Ecology, 9: 778-784.

Stoddart, D. M., 1976. Effect of the odour of weasels (*Mustela nivalis* L.) on trapped samples of their prey. Oecologia, 22: 439-441.

Stoddart, D. M., 1980. Some responses of a free living community of rodents to the odors of predators. Pages 1-10 *in* D. Müller-Schwarze & R. M. Silverstein (ed.). Chemical Signals: Vertebrates and Aquatic Invertebrates. Plenum Press, New York.

Stoddart, D. M., 1982. Does trap odour influence estimation of population size of the short-tailed vole, *Microtus agrestis*? Journal of Animal Ecology, 51: 375-386.

Strand, S. W. & W. M. Hamner, 1990. Schooling behavior of antarctic krill (*Euphausia superba*) in laboratory aquaria: Reactions to chemical and visual stimuli. Marine Biology, 106: 355-359.

Sullivan, T. P., 1986. Influence of wolverine (*Gulo gulo*) odor on feeding behavior of snowshoe hares (*Lepus americanus*). Journal of Mammalogy, 67: 385-388.

Sullivan, T. P. & D. R. Crump, 1984. Influence of mustelid scent-gland compounds on suppression of feeding by snowshoe hares (*Lepus americanus*). Journal of Chemical Ecology, 10: 1809-1821.

Sullivan, T. P. & D. R. Crump, 1986a. Avoidance reponse of pocket gophers (*Thomomys talpoides*) to mustelid anal gland compounds. Pages 519-531 *in* D. Duvall, D. Müller-Schwarze & R. M. Silverstein (ed.). Chemical Signals in Vertebrates IV: Ecology, Evolution and Comparative Biology. Plenum Press, New York.

Sullivan, T. P. & D. R. Crump, 1986b. Feeding responses of snowshoe hares (*Lepus americanus*) to volatile constituents of red fox (*Vulpes vulpes*) urine. Journal of Chemical Ecology, 12: 729-739.

Sullivan, T. P., D. R. Crump & D. S. Sullivan, 1988a. Use of predator odors as repellents to reduce feeding damage by herbivores. III. Montane and meadow voles (*Microtus montanus* and *Microtus pennsylvanicus*). Journal of Chemical Ecology, 14: 363-377.

Sullivan, T. P., D. R. Crump & D. S. Sullivan, 1988b. Use of predator odors as repellents to reduce feeding damage by herbivores. IV. Northern pocket gophers (*Thomomys talpoides*). Journal of Chemical Ecology, 14: 379-389.

Sullivan, T. P., L. O. Nordstrom & D. S. Sullivan, 1985a. The use of predator odors as repellents to reduce feeding damage by herbivores. I. Snowshoe hares (*Lepus americanus*). Journal of Chemical Ecology, 11: 903-919.

Sullivan, T. P., L. O. Nordstrom & D. S. Sullivan, 1985b. The use of predator odors as repellents to reduce feeding damage by herbivores. II. Black-tailed deer (*Odocoileus hemionus columbianus*). Journal of Chemical Ecology, 11: 921-935.

Sullivan, T. P., D. S. Sullivan, D. R. Crump, H. Weiser & E. A. Dixon, 1988. Predator odors and their potential role in managing pest rodents and rabbits. Pages 145-150 *in* A. C. Crabb & R. E. Marsh (ed.). Proceedings of the Vertebrate Pest Conference, University of California Davis, California.

Sullivan, T. P., D. R. Crump, H. Weiser & E. A. Dixon, 1990a. Response of pocket gophers (*Thomomys talpoides*) to an operational application of synthetic semiochemicals of stoat (*Mustela erminea*). Journal of Chemical Ecology, 16: 941-949.

Sullivan, T. P., D. R. Crump, H. Weiser & E. A. Dixon, 1990b. Comparison of release devices for stoat (*Mustela erminea*) semiochemicals used as montane vole (*Microtus montanus*) repellents. Journal of Chemical Ecology, 16: 951-957.

Suter, R. B., C. M. Shane & A. J. Hirscheimer, 1989. Spider *versus* spider: *Frontinella pyramitela* detects *Argyrodes trigonum* via cuticular chemicals. Journal of Arachnology, 17: 237-240.

Sweitzer, R. A. & J. Berger, 1992. Size-related effects of predation on habitat use and behavior of porcupines (*Erethizon dorsatum*). Ecology, 73: 867-875.

Swihart, R. K., 1991. Modifying scent-marking behavior to reduce woodchuck damage to fruit trees. Ecological Applications, 1: 98-103.

Swihart, R. K., J. J. Pignatello & M. J. I. Mattina, 1991. Aversive responses of white-tailed deer, *Odocoileus virginianus*, to predator urines. Journal of Chemical Ecology, 17: 767-777.

Szal, R., 1971. "New" sense organ of primitive gastropods. Nature, 229: 490-492.

Thoen, C., D. Bauwens & R. F. Verheyen, 1986. Chemoreceptive and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits. Animal Behaviour, 34: 1805-1813.

Tikkanen, P., T. Muotka & A. Huhta, 1994. Predator detection and avoidance by lotic mayfly nymphs of different size. Oecologia, 99: 252-259.

Tjossem, S. F., 1990. Effects of fish chemical cues on vertical migration behavior of *Chaoborus*. Limnology and Oceanography, 35: 1456-1468.

Tollrian, R., 1990. Predator-induced helmet formation in *Daphnia cucullata.* Archiv fur Hydrobiologie, 119: 191-196.

Tollrian, R., 1994. Fish-kairomone induced morphological changes in *Daphnia lumholtzi* (Sars). Archiv für Hydrobiologie, 130: 69-75.

Tollrian, R. & E. von Elert, 1994. Enrichment and purification of *Chaoborus* kairomone from water: Further steps toward its chemical characterization. Limnology and Oceanography, 39: 788-796.

Uiblein, F., J. R. Roca & D. L. Danielopol, 1994. Experimental observations on the behaviour of the ostracod *Cypridopsis vidua*. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnology, 25: 2418-2420.

Uiblein, F., J. R. Roca, A. Baltanas & D. L. Danielopol, 1996. Tradeoff between foraging and antipredator behaviour in a macrophyte dwelling ostracod. Archiv für Hydrobiologie, 137: 119-133.

Vadas, R. L., Sr., M. T. Burrows & R. N. Hughes, 1994. Foraging strategies of dogwhelks, *Nucella lapillus* (L.): Interacting effects of age, diet and chemical cues to the threat of predation. Oecologia, 100: 439-450.

VanDamme, R. & A. M. Castilla, 1996. Chemosensory predator recognition in the lizard *Podarcis hispanica*: Effects of predation pressure relaxation. Journal of Chemical Ecology, 22: 13-22.

VanDamme, R., D. Bauwens, D. Vanderstighelen & R. F. Verheyen, 1990. Responses of lizard *Lacerta vivipara* to predator chemical cues: The effects of temperature. Animal Behaviour, 40: 298-305.

Vander Meer, R. K., D. P. Jouvenaz & D. P. Wojcik, 1989. Chemical mimicry in a parasitoid (Hymenoptera: Eucharitidae) of fire ants (Hymenoptera: Formicidae). Journal of Chemical Ecology, 15: 2247-2261.

Vanhaaften, J. L., 1963. A natural repellent. Pages 389-392 *in* Nature Conservancy. International Union of Game Biologists, Transactions VI Conference, London.

Vernet-Maury, E., 1970. Excrétion urinaire des catécholamines chez le rat en fonction de l'ambiance olfactive. Journal of Physiology-Paris, 62: 461.

Vernet-Maury, E., 1980. Trimethyl-thiazoline in fox feces: A natural alarming substance for the rat. Page 407 *in* H. Van der Starre (ed.). Proceedings of the 7th International Symposium on Olfaction and Taste. IRL Press, London.

Vernet-Maury, E., B. Constant & J. Chanel, 1991. Repellent effects of trimethyl thiazoline in the wild rat *Rattus norevegicus* Berkenhout. Pages 305-310 *in* R. L. Doty & D. Müller-Schwarze (ed.). Chemical Signals in Vertebrates VI. Plenum Press, New York.

Vernet-Maury, E., A. Duveau & J. Chanel, 1982. Ontogeny of ultrasonic vocalizations in the rat after their alteration by fox odor. Abstract 5th ECRO Congress, Regensberg.

Vernet-Maury, E., E. H. Polak & A. Demael, 1984. Structure-activity relationship of stress-inducing odorants in the rat. Journal of Chemical Ecology, 10: 1007-1018.

Verrell, P. A., 1986. Male discrimination of larger, more fecund females in the smooth newt, *Triturus vulgaris*. Journal of Herpetology, 20: 416-422.

von Frisch, K., 1941a. Uber einen Schreckstoff der Fischhaut und seine Biologische Bedeutung. Zeitschrift fur vergleichende Physiologie, 29: 46-145.

von Frisch, K., 1941b. Die Bedeutung des Geruchsinnes im Leben der Fische. Naturwissenschaften, 22/23: 321-333.

Vuorinen, I., M. Ketola & M. Walls, 1989. Defensive spine formation in *Daphnia pulex* Leydig and induction by *Chaoborus crystallinus* DeGeer. Limnology and Oceanography, 34: 245-248.

Wahle, R. A., 1989. Chemically mediated predator avoidance in the American lobster, *Homarus americanus*. American Zoology, 29: 87A.

Wahle, R. A., 1992. Body-size dependent anti-predator mechanisms of the American lobster. Oikos, 65: 52-60.

Walls, M. & M. Ketola, 1989. Effects of predator-induced spines on individual fitness in *Daphnia pulex*. Limnology and Oceanography, 34: 390-396.

Walls, M., H. Caswell & M. Ketola, 1991. Demographic costs of *Chaoborus*-induced defenses in *Daphnia pulex:* A sensitivity analysis. Oecologia, 87: 43-50.

Washburn, J. O., M. E. Gross, D. R. Mercer & J. R. Anderson, 1988. Predator-induced trophic shift of a free-living ciliate: Parasitism of mosquito larvae by their prey. Science, 240: 1193-1195.

Watt, P. J. & S. Young, 1994. Effect of predator chemical cues on *Daphnia* behaviour in both horizontal and vertical planes. Animal Behaviour, 48: 861-869.

Webster, D. M., 1973. Audition, vision, and olfaction in kangaroo rat predator avoidance. American Zoology, 13: 1346.

Weider, L. J. & J. Pijanowska, 1993. Plasticity of *Daphnia* life histories in response to chemical cues from predators. Oikos, 67: 385-392.

Weldon, P. J., 1982. Responses to ophiophagous snakes by snakes of the genus *Thamnophis*. Copeia, 1982: 788-794.

Weldon, P. J., 1990. Responses by vertebrates to chemicals from predators. Pages 500-521 *in* D. W. MacDonald, D. Müller-Schwarze & S. E. Natynczuk (ed.). Chemical Signals in Vertebrates V. Oxford University Press, New York.

Weldon, P. J. & G. M. Burghardt, 1979. The ophiophage defensive response in crotaline snakes: Extension to new taxa. Journal of Chemical Ecology, 5:141-151.

Weldon, P. J., F. M. Divita & G. A. Middendorf III, 1987. Responses to snake odors by laboratory mice. Behavioural Processes, 14: 137-146.

Weldon, P. J., N. B. Ford & J. J. Perry-Richardson, 1990. Responses by corn snakes (*Elaphe guttata*) to chemicals from heterospecific snakes. Journal of Chemical Ecology, 16: 37-44.

Weldon, P. J., D. P. Graham & L. P. Mears, 1993. Carnivore fecal chemicals suppress feeding by alpine goats (*Capra hircus*). Journal of Chemical Ecology, 19: 2947-2952.

Whishaw, I. Q. & H. C. Dringenberg, 1991. How does the rat (*Rattus norvegicus*) adjust food-carrying reponses to the influences of distance, effort, predatory odor, food size, and food availability? Psychobiology, 19: 251-261.

Wiackowski, K. & M. Szkarlat, 1996. Effects of food availability on predator-induced morphological defense in the ciliate *Euplotes octocarinatus*. Hydrobiologia, 321: 47-52.

Wicklow, B. J., 1988. Developmental polymorphism induced by intraspecific predation in the ciliated protozoon *Onychodromus quadricornutus*. Journal of Protozoology, 35: 137-141.

Williams, D. D., 1986. Factors influencing the microdistribution of two sympatric species of Plecoptera: An experimental study. Canadian Journal of Fisheries and Aquatic Sciences, 43: 1005-1009.

Williams, D. D., 1990. A field study of the effects of water temperature, discharge and trout odour on the drift of stream invertebrates. Archiv fur Hydrobiologie, 119: 167-181.

Williams, D. D. & K. A. Moore, 1982. The effect of environmental factors on the activity of *Gammarus pseudolimnaeus* (Amphipoda). Hydrobiologia, 96: 137-147.

Williams, D. D. & K. A. Moore, 1985. The role of semiochemicals in benthic community relationships of the lotic amphipod *Gammarus pseudolimnaeus*: A laboratory analysis. Oikos, 44: 280-286.

Willman, E. J., A. M. Hill & D. L. Lodge, 1994. Response of three crayfish congeners (*Oronectes spp.*) to odors of fish carrion and live predatory fish. American Midland Naturalist, 132: 44-51.

Wilson, D. J. & H. Lefcort, 1993. The effect of predator diet on the alarm response of red-legged frog, *Rana aurora*, tadpoles. Animal Behaviour, 46: 1017-1019.

Yarnall, J. L., 1964. The responses of *Tegula funebralis* to starfishes and predatory snails. Veliger, 6 (Suppl.): 56-58.

Yentsch, C. S. & D. C. Pierce, 1955. "Swimming" anemone from Puget Sound. Science, 122: 1231-1233.

Ylönen, H. & H. Ronkainen, 1994. Breeding suppression in the bank vole as antipredatory adaptation in a predictable environment. Evolutionary Ecology, 8: 1-9.

Zagarese, H. E. & M. C. Marinone, 1992. Induction and inhibition of spine development in the rotifer *Keratella tropica*: Evidence from field observations and laboratory experiments. Freshwater Biology, 28: 289-300.

Zangrosi, H. & S. E. File, 1992. Behavioral consequences in animal tests of anxiety and exploration of exposure to cat odor. Brain Research Bulletin, 29: 381-388.