

Functional and Numerical Responses of Predators: Where Do Vipers Fit in the Traditional Paradigms?

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ABSTRACT

Snakes typically are not considered top carnivores, yet in many ecosystems they are a major predatory influence. A literature search confirmed that terrestrial ectotherms such as snakes are largely absent in most discussions of predator-prey dynamics. Here, we review classical functional and numerical responses of predator-prey relationships and then assess whether these traditional views are consistent with what we know of one group of snakes (true vipers and pitvipers: Viperidae). Specifically, we compare behavioural and physiological characteristics of vipers with those of more commonly studied mammalian (endothermic) predators and discuss how functional and numerical responses of vipers are fundamentally different. Overall, when compared to similar-sized endotherms, our analysis showed that vipers have: (i) lower functional responses owing primarily to longer prey handling times resulting from digestive limitations of consuming large prey and, for some adults, tolerance of fasting; (ii) stronger numerical responses resulting from higher efficiency of converting food into fitness currency (progeny), although this response often takes longer to be expressed; and (iii) reduced capacity for rapid numerical responses to short-term changes in prey abundance. Given these factors, the potential for viperids to regulate prey populations would most likely occur when prey populations are low. We provide suggestions for future research on key issues in predator-prey relationships of vipers, including their position within the classical paradigms of functional and numerical responses.

Key words: *Crotalus atrox*, endotherms, ectotherms, functional response, prey regulation, numerical response, predator-prey dynamics, reptiles, Viperidae.

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I. INTRODUCTION

The term “predator” often evokes images of animals such as lions and weasels rather than snakes, although the latter play similarly important roles, and in a variety of habitats snakes are, or are among, the top predators (Brischoux, Bonnet & Shine, 2007), particularly on islands (Savidge, 1987; Sun *et al.*, 2001; Wüster, Duarte & Salomão, 2005). All snakes are carnivorous and in some ecosystems they are, or were, among the largest and/or most common predators (Fitch, 1960, 1999; Klauber, 1972; Godley, 1980; Albino, 1993; Greene, 1997; Sun *et al.*, 2001; Himes, 2002). By their sheer collective biomass alone, snakes may exert considerable predatory pressure on prey populations (Godley, 1980; Reichenbach & Dalrymple, 1986; Stewart & Woolbright, 1996; Petranksa & Murray, 2001; Franzreb, 2007). As a result, when introduced into previously snake-free systems, these predators can have devastating consequences for prey populations (Savidge, 1987; Rodda *et al.*, 1999).

Of the approximately 3000 extant snake species, about 235 are vipers (Viperidae) and some of these exceed 2 m in total length and 1 kg in body mass (Greene, 1997). There is a substantial literature detailing diet, foraging, feeding behaviour, and energetics of vipers (Fitch 1948, 1960; Klauber, 1972; Pomianowska-Pilipiuk, 1974; Beavers, 1976; Pough & Groves, 1983; Duvall, King & Gutzwiller, 1985; Duvall *et al.*, 1990a, b; Wallace & Diller, 1990; Greene, 1983, 1992, 1997; Arnold, 1993; Secor & Nagy, 1994; Beaupre, 1995a, b, 1996, 2002; Beck, 1995; Roth, May & Farrell, 1999; Theodoratus & Chiszar, 2000; Cundall, 2002; Martins, Marques & Sazima, 2002; Shine & Sun, 2003; Clark, 2004, 2006; Ineich *et al.*, 2006). Given their abundance and relatively large size, viper predators are likely to be important drivers of energy flow in the ecosystems they occupy (Fitch, 1960; Pomianowska-Pilipiuk, 1974; Tanaka, Hayashi & Wada, 1999).

Traditionally, predator-prey relationships have been viewed in light of how the number of prey consumed changes with increasing prey abundance (functional responses) and how predator populations change with increasing prey abundance (numerical responses), the classical theoretical constructs originally developed by C.S. Holling based primarily on small mammalian predators and their

invertebrate prey (Holling, 1959a, b). Although behaviour of ectothermic vertebrate predators may broadly conform to these models, in many respects the fundamental differences between ectotherms and endotherms in energy use and allocation could lead to divergent responses. This especially may hold true for vipers, many of which show extreme capacities in energy efficiency and “low energy” lifestyles (Pough, 1980; Greene, 1983, 1997; Pough & Groves, 1983; Secor & Nagy, 1994; Capizzi & Luiselli, 1996; Bonnet, Bradshaw & Shine, 1998; Beaupre, 2002; Cundall, 2002; Shine, 2005).

Although the diet, foraging behaviour, and energetics of vipers have been well-documented, we could find no papers that explicitly studied or predicted the functional responses of viper predators to prey. Likewise, while reproductive responses of vipers to prey abundance have been examined for a few species, including cottonmouth (*Agkistrodon contortrix*; Fitch, 1960), western rattlesnake (*Crotalus oreganus*; Diller & Johnson, 1988), adder (*Vipera berus*; Forsman, 1991; Forsman & Lindell, 1997), aspic viper (*Vipera aspis*; Lourdaïs *et al.*, 2002), and western diamond-backed rattlesnake (*Crotalus atrox*; Taylor *et al.*, 2005), this literature has not been placed in a framework to examine functional and numerical responses. Here, our goal was to review and develop a context for the nature and effects of vipers as predators, in light of the lack of published information on their numerical and functional responses. We have chosen to spotlight temperate vipers due to the relative abundance of published studies describing their life and natural histories (reviewed by Greene, 1997; Shine & Bonnet, 2000). First, we review functional and numerical responses in predator-prey relationships for classically studied predators. We then contrast unique physiological and behavioural characteristics of vipers to selected mammalian endothermic species. Next, drawing on results of a long-term (> 12 years) field study of western diamond-backed rattlesnakes, we infer potential viper functional and numerical responses in comparison to mammalian predators which are similar-sized and/or consume similar prey species, and hypothesize effects of vipers on prey populations. Last, we discuss the robustness of classical paradigms to functional and numerical responses of predator-prey relationships when considering vipers, and suggest future directions for research on predator-prey relationships of vipers.

II. LITERATURE REVIEW

To determine whether terrestrial ectotherms are under-represented in the predator-prey literature, we conducted an electronic search using CSA Illumina – Biological Sciences (©CSA 2006) with the key words ‘predator-prey relationships’ and ‘predator-prey theory’ in December 2006. In total, 383 unique abstracts were returned. Of these, we excluded 15 papers dealing with consumers feeding on producers (e.g. plants or phytoplankton), one paper that appeared to have no relevance to predator-prey relationships, and 47 papers that did not contain original research (theoretical modeling papers, review papers, book chapters, and symposia overviews). Additional searches were performed using *Web of Science* (1955–2007), using the terms ‘functional response’ and ‘numerical response’ in conjunction with various taxonomic terms limited to Reptilia, e.g. Serpentes and Crocodylia. One study was returned, on the numerical responses of terrestrial ectotherms (lizards), which appeared to define a numerical response as the temporary immigration of adults into an area to consume hatching aquatic insects (Sabo & Power, 2002), in contrast to previous definitions (Solomon, 1949; Holling, 1959a, b; Taylor, 1984).

Of 320 papers containing original field-based research, seven abstracts discussed predator behaviour or abundance without listing specific prey species, and 12 abstracts discussed experimental manipulations of prey anti-predator behaviours or survival without listing the predator. Of the remaining 301 papers, 76 were studies of marine, freshwater aquatic, a combination of marine and freshwater, or terrestrial food webs (including multi-trophic fishery studies), while 225 detailed single trophic-level relationships (Table 1). We determined which predator and prey species were featured in these relationships. For simplicity, we divided predator and prey species into three discrete categories: (1) invertebrate or vertebrate; (2) terrestrial, marine, or freshwater aquatic; and (3) endothermic or ectothermic (Table 1). Humans exploiting fish and polar bears were placed with terrestrial endotherms, seals and sea lions were placed with marine endotherms, tuna were placed with marine ectotherms (recognizing this is controversial owing to information on their thermoregulation capabilities), larval amphibians and aquatic turtles were placed with freshwater aquatic ectotherms, and parasites and zooplankton were placed with invertebrates.

In the foodweb papers, predators typically fit into multiple categories, i.e. one paper would include predators from terrestrial endotherm, marine endotherm, and marine ectotherm categories. Of the 225 single trophic-level interaction papers, 74 or 32.9% involved marine ectothermic vertebrate predators, 46 (20.4%) involved marine invertebrate predators, 37 (16.4%) involved freshwater aquatic ectothermic vertebrate predators, 27 (12.0%) involved terrestrial endothermic vertebrate predators, 24 (10.7%), involved freshwater aquatic invertebrate predators, 16 (7.1%) involved terrestrial invertebrate predators, and one (0.4%) involved marine endothermic predators (Table 1). No studies involved predators that were terrestrial ectothermic

vertebrates. One study examined vipers as prey, a tangential study of the anti-predatory defences of cottonmouths (*Agkistrodon piscivorus*) when threatened by human predators (Roth & Johnson, 2004).

Although our searches were not exhaustive, they were sufficiently large to support the contention that predator-prey studies have traditionally focused on relatively few taxa, and that terrestrial ectothermic vertebrates are under-represented in proportion to their biodiversity (e.g. May, 1988; Bonnet *et al.*, 1998; Shine & Bonnet, 2000). Thus predator-prey models developed to date may not adequately reflect the nature of predator-prey relationships in terrestrial ectotherms. This may be a function of the difficulty in studying population dynamics, predation behaviour, feeding events, and mortality in hard-to-find taxa such as vipers (e.g. Erwin, 1989). However, recent advances in individual identification (e.g. marking), radio-telemetric techniques (Shine & Bonnet, 2000), observational technologies such as remote videocameras (e.g. Clark, 2006), and increasing forensic capabilities with scats (e.g. Beaupre, 1995a; Corbett & Newsome, 1987; Eide *et al.*, 2005; Holycross *et al.*, 2002; Prival *et al.*, 2002) are facilitating field studies of traditionally hard-to-study species. Thus, we can begin to make predictions for predator-prey relationships for one relatively well-studied group of terrestrial ectotherms — temperate vipers.

III. BACKGROUND: FUNCTIONAL AND NUMERICAL RESPONSES

(1) Functional responses

Holling (1959a, b) defined the term ‘functional response’ (after Solomon, 1949) as an increase in the number of prey consumed in response to increasing prey population density and recognized three major types of predator responses (Fig. 1). These responses differed from earlier Lotka-Volterra models (e.g. Taylor, 1984) because they assumed satiation by predators (physical and/or behavioural) at high prey densities, resulting in stabilization of predation rates. Type I responses would be shown by predators that searched randomly for prey and maintained search at a constant level across prey densities until satiation (Holling, 1959a; Fig. 1A). Examples of this response have been demonstrated for Canada lynx (*Lynx canadensis*) predation on snowshoe hare (*Lepus americanus*) (Brand, Keith & Fischer, 1976), and for stoat (*Mustela erminea*) and least weasel (*Mustela nivalis*) responding to vole (*Microtus* spp. and *Clethrionomys glareolus*) densities (Korpimäki, Norrdahl & Rinta-Jaskari, 1991). Type II responses involve an initial rapid increase in the number of prey taken per predator, followed by a progressively slower rate due to either the time-consuming nature of prey handling and digestion, or satiation (Holling, 1959a; Taylor, 1984; Fig. 1B). The Type II response has been demonstrated for least weasel (*Mustela nivalis*) feeding on voles (Sundell *et al.*, 2000), dingo (*Canis familiaris dingo*) eating European rabbit (*Oryctolagus cuniculus*), small mammals, and carcasses of taurine cattle (*Bos taurus*) (Corbett &

Table 1. Relative number of 301 original abstracts discussing predator and prey interactions, found using the electronic search engine CSA Illumina – Biological Sciences (©CSA 2006) with the key words “predator-prey relationships” and “predator-prey theory” on December 15, 2006. Predator and prey species are divided into three discrete types: (1) invertebrate or vertebrate; (2) terrestrial, marine, or freshwater aquatic; and (3) endothermic or ectothermic. “–” indicates that no records were found fitting the categories. Numbers in parentheses indicate fossil relationships; these are included in the totals to their left

	Vertebrate Prey					Invertebrate Prey		
	Terrestrial endotherm	Terrestrial ectotherm	Freshwater aquatic	Marine endotherm	Marine ectotherm	Terrestrial	Freshwater aquatic	Marine
Vertebrate Predator								
Terrestrial endotherm	13 (1)	1	3	2	2	5	—	1
Terrestrial ectotherm	—	—	—	—	—	—	—	—
Freshwater aquatic ectotherm	—	—	19	—	—	—	18	—
Marine endotherm	—	—	—	—	1	—	—	—
Marine ectotherm	—	—	—	—	33 (1)	—	—	41
Invertebrate Predator								
Terrestrial	3	—	—	—	—	13	—	—
Marine	—	—	—	—	3	—	—	43 (1)
Freshwater aquatic	—	—	2	—	—	—	22 (1)	—
Foodwebs								
Terrestrial	4							
Marine	39							
Aquatic	30							
Marine + aquatic	3							

Newsome, 1987). Type III responses show an initially slow increase in the number of prey taken as density increases, followed by a rapid increase that slows to a plateau, producing a sigmoidal (S-shaped) curve (Holling, 1959*a, b*, Fig. 1C). The initially low number of prey taken with increasing prey density has been hypothesized to be the result of the predator's learning to recognise or capture prey (Holling, 1959*a, b*; Tinbergen, 1960; Fraser & Hoffman, 2003), or alternating between prey species (Oaten & Murdoch, 1975*a, b*; Pech, Sinclair & Newsome, 1995; Schmitz, 1995; Kjellander & Nordström, 2003). Many studies of mammals have shown this response in nature, e.g. coyote (*Canis latrans*) eating snowshoe hare (Todd, Keith & Fischer, 1981 as redrawn by Boutin, 1995), red fox (*Vulpes vulpes*) eating European rabbit (Pech *et al.*, 1992), and polecat (*Mustela putorius*) feeding on agile frog (*Rana dalmatina*) (Lode, 2000).

Many factors influence the shape of functional response curves, for example optimal foraging theory and its derivations (e.g. fractal geometry); these and related topics are ably discussed elsewhere (e.g. MacArthur & Pianka, 1966; Charnov, 1976; Belovsky, Ritchie & Moorhead, 1989; Erwin, 1989; Schmitz, 1995; Ritchie, 1998; Jepsen *et al.*, 2002; Pitt & Ritchie, 2002; Křivan & Vrkoč, 2004; Eide *et al.*, 2005; Johnson, 2006; Overholtzer-McLeod, 2006). More recently, the idea that the functional response of predators is primarily dependent on the density of prey has been challenged (Abrams & Ginzburg, 2000). According to the alternative “ratio-dependent,” or “predator-dependent” hypothesis, the functional response depends on the ratio of the prey population size to the predator population size.

These responses have been demonstrated in studies of cod (*Gadus morhua*) predation on young sprat (*Sprattus sprattus*; Essington & Hansson (2004), and banded sunfish (*Enneacanthus obesus*) predation on southern leopard frog (*Rana sphenoccephala*) tadpoles (Chalcraft & Resetarits, 2004). Abrams & Ginzburg (2000) and Vucetich, Peterson & Schaefer (2002) surmised that strict prey-dependent or predator-dependent functional responses are rare in nature.

(2) Numerical responses

Both Solomon (1949) and Holling (1959*a, b*) demonstrated that predators have numerical responses — defined as changes in predator numbers based on reproductive recruitment — in response to increasing prey density. Numerical responses are well documented for predators of cyclic small mammal populations. These include various mammal, owl and raptor predators feeding on cycling snowshoe hare populations (Brand *et al.*, 1976; Keith *et al.*, 1977); mustelids, owls and kestrels feeding on several cyclic vole species (Erlinge *et al.*, 1983; Korpimäki *et al.*, 1991; Korpimäki & Norrdahl, 1991, and reviewed by Hanski & Henttonen, 1996, Sundell *et al.*, 2000); and red fox feeding on European rabbit (Pech *et al.*, 1992). Numerical responses are not well documented for predators of non-cyclic prey, but are known in grey wolf (*Canis lupus*) populations that prey on moose (*Alces alces*; Messier, 1994), mustelids consuming non-cyclic vole species (Hanski & Henttonen, 1996), and in Adelie penguin (*Pygoscelis adeliae*) and various seabirds feeding on Antarctic krill (*Euphausia superba* cascade; Fraser & Hoffman, 2003).

(3) Total responses

Holling (1959a) defined the term 'total response' as the sum of numerical and functional responses and pointed out that the potential for predators to regulate prey populations depended on the interaction between functional and numerical responses. Gilg *et al.* (2006), studying the functional and numerical responses of predators (two bird and two mammal species) to cycling collared lemmings (*Dicrostonyx groenlandicus*), point out that the complexity of predators' impacts on prey populations occurs because predators respond functionally to current prey densities but respond numerically to past prey densities, thus causing the delayed time-lag often seen in predators' numerical responses (see also Keith *et al.*, 1977; Erlinge *et al.*, 1983; Kjellander & Nordström, 2003).

IV. COMPARATIVE ECOLOGY OF VIPERS AND MAMMALIAN PREDATORS

(1) Physiology: endothermy versus ectothermy

In general, ectotherms have low metabolic rates and high efficiencies for converting assimilated energy to new biomass (Pough, 1980; Spotila & Standora, 1985; Reichenbach & Dalrymple, 1986; Bonnet *et al.*, 1998; Shine, Fitzgerald & Kearney, 2003; Nagy, 2005; Shine, 2005). Moreover, they vary in energetic efficiency depending on ambient temperatures, prey type, prey size, and foraging mode (Pough, 1980; Spotila & Standora, 1985; Secor & Nagy, 1994; Forsman, 1996; Lillywhite, 1993; Beaupre, 2002; Dorcas, Hopkins & Roe, 2004; Nagy, 2005; Ineich *et al.*, 2006). Overall, net efficiency of energy conversion to biomass in ectotherms ranged from 6 to 98% while that of endotherms ranged from 0.50 to 3.0% (Pough, 1980). For example, least weasel averaged 2.3% net efficiency, compared to 41–49% for similarly sized syntopic adder (Pomianowska-Pilipiuk, 1974; Pough, 1980).

One consequence of this difference in metabolic efficiency is that highly energy-efficient ectothermic vipers have lower daily energy needs than similar-sized endotherms. Carbone, Teacher & Rowecliffe (2007) predicted that [endothermic] carnivores ranging in mass from 0.1–1 kg would require between 200 and 1200 kJ per day to meet maintenance requirements, yet field research indicates these numbers may be high. Non-breeding female black-footed ferrets (*Mustela nigriceps*) required 58 kJ/kg mass per day for maintenance (46.4 kJ total; Stromberg, Rayburn & Clark, 1983), while energy consumption in male coyotes averaged 24 kJ/kg per day (279.6 kJ total; Laundre & Hernandez, 2003), and bobcats (*Lynx rufus*) kept in captivity consumed an average of 21–24 kJ/kg per day (190 kJ total; Golley *et al.*, 1965). Smaller mammalian predators, like ermine (*Mustela erminea*) and least weasels, had daily energetic costs ranging from 350–720 kJ/day and 180–380 kJ/day, respectively (Chappell, 1980). By contrast, entire active-season energy budgets for viperids can be less than mammalian daily energy budgets. Pomianowska-Pilipiuk (1974) estimated

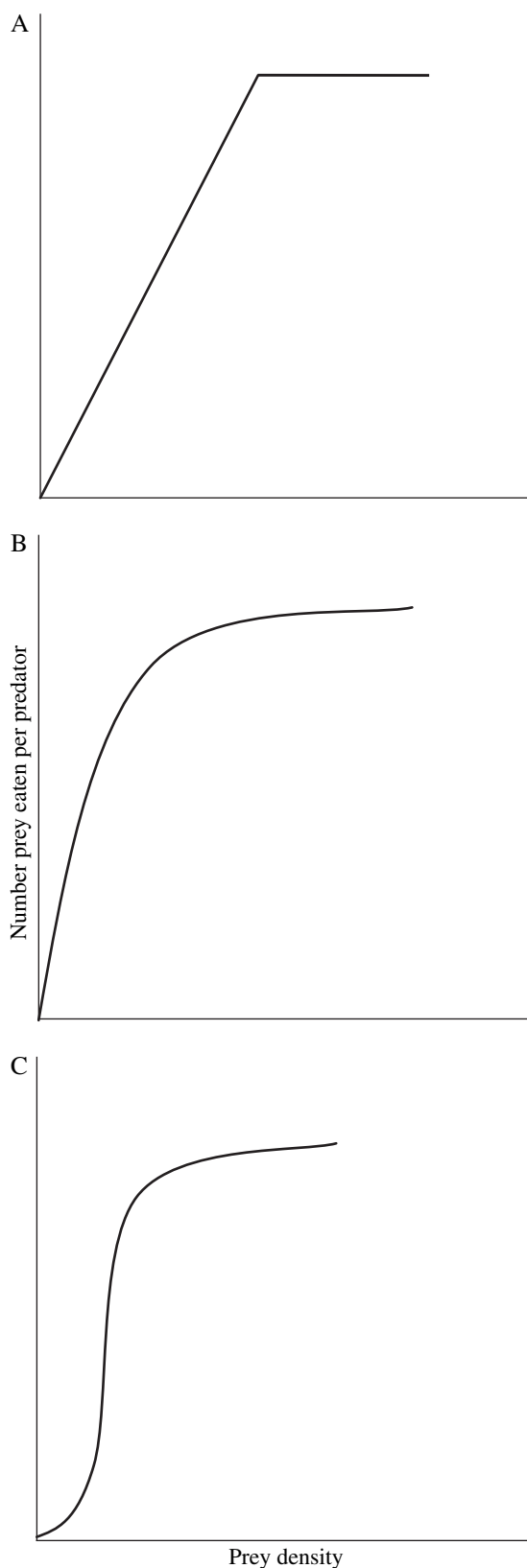


Fig. 1. Type I (A), Type II (B), and Type III (C) predator functional responses in relation to prey density, as defined by Holling (1959a).

energy requirements of 83.6 kJ per annum for male adders (13 kJ/kg/day), while Dorcas *et al.*, (2004) estimated annual energy requirements of 3494 and 12684 kJ (3.49 and 3.17 kJ/kg) for a 1 kg and 4 kg eastern diamond-backed rattlesnake (*C. adamanteus*) at 25°C, respectively, and Beaupre (1995*b*, 1996) estimated summer (three months) energy requirements of 655–1116 kJ for male mottled rock rattlesnakes (*C. lepidus*; 7.34–13.0 kJ/kg/day).

The relatively stout body size (large mass:length ratio) of many adult vipers may further increase their capacity for per-unit-mass energy storage compared to other ectotherms (e.g. Greene, 1983; Pough & Groves, 1983; Arnold, 1993; Secor, Stein & Diamond, 1994; Cundall, 2002). As well, the ability to retain digesta over a period of weeks may enhance the energetic efficiency of digestion (Secor & Diamond, 2000; Lillywhite, De Delva & Noonan, 2002). Some adult vipers have been shown to tolerate long-term fasting (Sun *et al.*, 2002; McCue, 2007), further stretching this long-term energy storage capacity.

Young vipers have higher energy requirements than adults, largely because of energetic allocations focusing on rapid growth rather than storage (Beaupre & Zaidan, 2001). For example, Dorcas *et al.* (2004) calculated that a 1 kg (juvenile) eastern diamond-backed rattlesnake would need to consume between 0.33 and 6.80 rodent meals (given ambient temperatures of 5 and 35°C, respectively) to meet annual standard metabolic rate (SMR) costs; while a 4 kg snake (adult) would require between 0.30 (5°C) and 6.17 (35°C) rodents per year to meet annual standard metabolic costs. Diller & Johnson (1988) estimated that first-year western rattlesnakes would need to consume prey mass equal to three times their body mass, whereas adults required a prey mass 1.6 times their body mass. The higher energetic efficiency of young snakes relative to adults has been documented in several species (e.g. Diller & Johnson, 1988). However, juvenile vipers may also differ in their energy allocations to growth both between and within species, depending on maternal yolk provisioning, food availability, and abiotic factors such as elevation, temperature, and latitude (Macartney, Gregory & Charland, 1990; Bonnet *et al.*, 1998, 2001; Beaupre & Zaidan, 2001; Beaupre, 2002).

(2) Comparative biomass consumption and feeding rates

Given low energy requirements and/or high energy efficiency, it is not surprising that feeding rates for adults in many species of temperate vipers are also low compared to similar-sized endotherms and even many ectotherms (Bonnet *et al.*, 1998; Secor & Diamond, 2000; but see Mori, Toda & Ota, 2002; Ineich *et al.*, 2006). Similarly sized mustelids have body shapes generally similar to vipers, proportions which confer high energetic requirements in endotherms (Brown & Lasiewski, 1972; Greene, 1997). Non-reproductive least weasels may consume 4–20 prey per week (Jędrzejewska & Jędrzejewski, 1989) while the data available for vipers suggest that individual predation rates are significantly lower, usually less than one prey animal per week (Table 2), and in some

populations of vipers, only a few meals per annum (Fitch, 1948, 1960; Greene, 1986, 1997; Secor & Nagy, 1994; Beck, 1995; Bonnet *et al.*, 1998; Sun *et al.*, 2002; Shine *et al.*, 2003; Dorcas *et al.*, 2004). Fitch (1948) estimated that a [non-pregnant] adult western rattlesnake (for taxonomic changes see Douglas *et al.*, 2002) would need to consume a prey mass equal to twice its mass each year for growth and maintenance. Rattlesnakes typically consume annual prey mass equal to 95–100% of their respective body masses to meet maintenance requirements (Beck, 1995; Clark, 2006); however, individual adult mottled rock rattlesnakes consume a prey mass equal to 113–195% of their body mass per annum for growth and maintenance, or 82% of annual assimilated energy (Beaupre, 1996). By contrast, potentially syntopic male and non-reproductive female black-footed ferrets require a minimum annual prey mass (white- or black-tailed prairie dogs, *Cynomys leucurus* or *C. ludovicianus*) that is 42,186% their body mass to meet maintenance requirements (after Stromberg *et al.*, 1983). Non-reproductive least weasel in Poland annually consume a minimum average prey mass of 13,165% of their (average non-reproductive) mass per annum (91 g; calculated from Jędrzejewski, Jędrzejewska & Szymura, 1995).

(3) Prey:predator size ratios

For many mammalian predators the ratio of prey mass to predator mass is less than 0.5 (e.g., Carbone *et al.*, 2007), but prey-predator mass ratios may exceed this in large felids, as well as in some vipers (Greene, 1983, 1992, 1997; Arnold, 1993; Schuett, Nowak & Repp, 2002) (Table 2). Unlike most mammalian predators, vipers are morphologically and physiologically adapted for swallowing whole relatively large prey, with subsequent digestion requiring 1–3 weeks (Cundall, 2002; Fitch, 1960; Greene, 1986, 1992, 1997; Pough & Groves, 1983; Secor & Nagy, 1994; Lillywhite *et al.*, 2002; E.M. Nowak, unpublished data). In addition to theoretically high cost-benefit ratios associated with large animals infrequently consuming small prey (e.g. Arnold, 1993; Forsman, 1996; Lillywhite *et al.*, 2002), digestive function in large-bodied snakes (e.g. intestinal mass, nutrient uptake capacity) appears to decline between large meals, resulting in high costs of “restarting” the digestive system (Secor *et al.*, 1994; Secor & Diamond, 2000). One outcome of this adaptation is that on reaching maximal size as adults, some large-bodied vipers appear rarely to feed on small prey in the wild (predicted by Belovsky *et al.*, 1989), in one case even when prey was offered experimentally (Shine & Sun, 2003). Due to difficulties with detecting small or quickly digested prey in stout-bodied vipers, and given that some species of vipers are documented to eat small prey as adults (e.g. Clark, 2002; Martins *et al.*, 2002; Mori *et al.*, 2002; Ineich *et al.*, 2006), how generally applicable this pattern is remains to be determined.

A review of the metabolic costs of prey-predator mass ratios among terrestrial endotherms (Carbone *et al.*, 2007) suggests that large felids and canids are most similar to large viper species in primarily consuming very large prey relative to their own body mass (Mills & Shenk, 1992; Mills & Biggs,

Predator	Life span (years)	# progeny per litter	# litters per year	Range size	Main prey species	# Prey eaten per week or [as published]	Prey mass (kg)	Predator mass (kg)	Prey: predator mass ratio	% Prey biomass removed per year	References
African lion (savanna Africa) <i>Leo panthera</i>	12-16	1-4	0.5	22.6-82.7 km ² (a)	Blue wildebeest <i>Connochaetes taurinus</i>	0.1	145-162	124-188	1.2-2.0	42%	IUCN (2006); Kissui & Packer (2004); Mills & Biggs (1993); Mills & Shenk (1992); Radloff & Du Toit (2004); Spong (2002); IUCN (2006); Mizutani & Jewell (1998); Radloff & Du Toit (2004)
Leopard (savanna Africa) <i>Panthera pardus</i>	12-15	1-4	0.5-0.8	f = 20.7 km ² *	Impala <i>Aepyceros melampus</i>	[47-48% of diet]	30.9-35.5	37.3-61.3	0.8-0.6	n/a	IUCN (2006); Mizutani & Jewell (1998); Radloff & Du Toit (2004)
Mountain lion (CA, USA) <i>Puma concolor</i>	12-13	3	0.71	f = 69.9 km ² , m = 193.4 km ²	Mule deer <i>Odocoileus hemionus</i> , Elk <i>Cervus canadensis</i>	0.7-1	50-100	40-70	1.2-1.4	n/a	Logan & Sweanor (2001); J. Hart (pers. comm.)
Canada lynx (Canada) <i>Lynx canadensis</i>	15	1-4	1	11.1-49.5 km ²	Snowshoe hare <i>Lepus americanus</i>	[0.2-0.8 per day] (c)	1.2-1.4	8.6	0.1-0.2	n/a	Brand <i>et al</i> (1976); IUCN (2006)
Polecat (Europe) <i>Mustela putorius</i>	10-14	8-9	1-2	0.4-1.5 km ²	Aogle frog <i>Rana dalmatina</i>	[13.8-15.5% of diet]	0.02*	0.7-1.1	0.02-0.04	n/a	Lode (2000); Marcelli <i>et al</i> (2003); Mead & Wright (1983)
Least weasel (Europe) <i>Mustela nivalis</i>	1-3	4-5	2	1-216 ha	Bank vole <i>Clethrionomys glareolus</i>	4.0-19.5	0.03*	0.04-0.2	0.1-0.7	2-28% per autumn	Jedrzejewski (1989); Jedrzejewski <i>et al</i> , (1995); Sheffield & King (1994)
Bushmaster (Costa Rica) <i>Lachesis muta</i>	20?	7-10	1-2*	n/a	Rats (species not given)	0.1-0.2	≤ 50% of snake	2-4	Generally ≤ 0.5	n/a	Fitch (1970); Greene (1986, 1997)
Adder (Sweden) <i>Vipera berus</i>	20	10-12	0.5	800-1500 m from dens	Rodents, esp. voles (various)	0.96	0.008-0.02	f = 0.1	0.1-0.2	18% per ha for voles*	Forsman & Lindell (1997); Pomianowska-Pilpiuk (1974)

Table 2. (cont.)

Predator	Life span (years)	# progeny per litter	# litters per year	Range size	Main prey species	# Prey eaten per week or [as published]	Prey mass (kg)	Predator mass (kg)	Prey: predator mass ratio	% Prey biomass removed per year	References
Timber rattlesnake (NY, USA) <i>Crotalus horridus</i>	16-22	4-14	≥ 0.3 (b)	17-65 ha	Woodland rodents (various)	0.6-0.8	0.05-0.3	0.6-2.1	0.02-0.5	41-58 squirrels and 168-209 mice per year*	Brown (1991, 1993); Clark (2006)
Copperhead (KS, USA) <i>Agkistrodon contortrix</i>	18	4-13	0.5	m = 1.6, f = 1.9 ha	Mice (various) and voles (<i>Microtus</i> spp.)	0.4	0.01 (mice)-0.03 (vole)	0.1-0.7	0.04-0.1	? over 453 kg per year	Fitch (1960, 1999)
Western rattlesnake (CA, USA) <i>C. oreganus</i>	20-25**	10	0.5	n/a	Juvenile California ground squirrels <i>Citellus beecheyi</i>	0.05-0.1*	0.2-0.4*	0.2	0.5-1.0+	13-26% per acre* (d)	Fitch (1948, 1970)
Western diamond-backed rattlesnake (Tonto NM, AZ, USA) <i>C. atrox</i>	20-25	3-5	0.5	6.0-19.0 ha (≥ 1 year)	Rodents (Bailey's pocket mouse <i>Chaetodipus baylei</i> , <i>Peromyscus</i> spp., woodrat <i>Neotoma albigula</i>)	0.7 (mice)-0.06 (woodrat)	0.04 (mice)-0.2 (woodrat)	0.4-0.5	0.1-0.3	n/a	E.M. Nowak unpublished data
Western diamond-backed rattlesnake (Montezuma Castle NM, AZ, USA)	20-25	3-5	0.5	6.0-19.0 ha (≥ 1 year)	Woodrat, rabbits <i>Sylvilagus</i> sp.	0.7 (woodrat)-0.07 (rabbit)	0.1 (woodrat)- (rabbit)	0.5-1.1	0.3-1.0+	n/a	Nowak (2005); Nowak & van Riper (1999); E.M. Nowak unpublished data

(a) Activity range size is given per pride, not per individual. Range size is estimated by the 90% adaptive kernel method.

(b) Most females in this population did not breed until they were 9-10 years old.

(c) Some of the kills were made by mothers with kittens; data from winters only.

(d) Calculated by: number of squirrels per acre (23) x averaged % of young adult squirrels in the population measured during months when snakes could be active (32.5%).

1993; Logan & Sweanor, 2001; Radloff & Du Toit, 2004; Henschel, Abernethy & White 2005). Prey-predator mass ratios average at least 1:1 for female and 2.1:1 for male African lion (*Leo panthera*; recognizing that individual prey are typically killed by several pride members; Mills & Biggs, 1993), 0.8:1 for female and 0.6:1 for male leopard (*Panthera pardus*) in South Africa (Radloff & Du Toit, 2004; Table 2), and 1.2 to 1.4 for mountain lion (*Puma concolor*) in Flagstaff, Arizona (J. Hart, personal communication; Table 2). For endothermic species that consume the same endothermic prey as many temperate viperids (e.g. rodents and lagomorphs), prey:predator mass ratios are much smaller: several mustelids range from 0.02 to 0.75 (Marcelli, Fusillo & Boitani, 2003; Sheffield & King, 1994; Table 2); and those of Canada lynx range from 0.1 to 0.2 (Brand *et al.*, 1976; G. Merrill, personal communication; Table 2).

(4) Foraging strategies and activity range use patterns

Perhaps due to a tendency to eat relatively few meals per annum (e.g. Dorcas *et al.*, 2004; Clark, 2006), temperate vipers generally show a high degree of fidelity to both foraging and retreat sites and are fairly sedentary (Secor & Nagy, 1994; Nowak & van Riper, 1999; Nowak, Hare & McNally, 2002; Nowak, 2005). These vipers differ from similar-sized terrestrial endotherms (e.g. mustelids, small felids and canids) in that they are less likely to be active foragers, and tend to forage over smaller areas (Secor & Diamond, 2000; but see Ineich *et al.*, 2006). Viper hunting styles parallel that of some large endothermic ambush predators like leopards (Henschel *et al.*, 2005) and African lions (Hopcraft, Sinclair & Packer, 2005); vipers may also be considered classic “sit-and-wait” predators (Pough & Groves, 1983; Arnold, 1993; Bonnet *et al.*, 1998). Cooper (2005, 2007) notes that the classic dichotomy between ambush and active foraging might best be viewed as a continuum of foraging modes, and Greene (1992) coined the term “mobile ambushers” for those viper species that make long-distance migrations to their foraging grounds (e.g. prairie rattlesnake *C. v. viridis*, Duvall, King & Gutzwiller, 1985). Regardless, it is not uncommon for individual vipers to stay in the same foraging area for several days or longer (Duvall *et al.*, 1985; Secor & Nagy, 1994; Greene, 1997; Bonnet *et al.*, 1998; Nowak & van Riper, 1999; Clark, 2006). One of us (E.M. Nowak, unpublished data) observed a healthy radio-telemetered western diamond-backed rattlesnake remain in a hunting coil apparently without moving for eight days, even when a rain storm caused small leaves to fall on her (based on daily locations).

Viper home range sizes are variable in comparison to similar-sized mammalian predators (Table 2), but typically differ in overall shape and in concentration of core use areas. Temperate viper home ranges typically consist of two or more core use areas, one centered on the hibernation location, and one or more centered within the summer foraging area (Macartney, Gregory & Larsen, 1988); there may (e.g. Duvall *et al.*, 1990b) or may not be (e.g. Nowak & van Riper, 1999) long dispersal movements between core

areas. Large-bodied female Canada lynx (1.2–1.4 kg) have home range sizes of 11.1–49.5 km² (Brand *et al.*, 1976), while medium-sized adult European polecats, *Mustela putorius* (0.68–1.11 kg) had activity ranges of 0.39–1.48 km² over four to six months (Lode, 2000). Male vipers (e.g. 0.55–1.1 kg in populations studied by the authors) typically cover several kilometers annually, either during seasonal straight-line dispersal movements (e.g. Duvall *et al.*, 1990b) or within polygon-shaped ranges (e.g. Nowak & van Riper, 1999; Nowak, 2005), ranges which are similar to or smaller than those noted by Brand *et al.*, (1976) and Lode (2000). However, female vipers (e.g. 0.41–0.55 kg in populations studied by the authors) may have ranges with diameters less than 0.05 km² (Nowak & van Riper, 1999), more similar to those of 0.04–0.22 kg least weasel, which have annual home ranges of 0.01–2.16 km² (Sheffield & King, 1994; Jędrzejewski *et al.*, 1995). Viperid home ranges frequently overlap within species, and there appear to be few antagonistic interactions between species (e.g. Beck, 1995; Forsman & Lindell, 1997; Nowak & van Riper, 1999; Nowak, 2005; Taylor *et al.*, 2005; G.W. Schuett, unpublished data).

(5) Life-history strategies

Life-history strategies of vipers are different from most mammalian endotherms, regardless of body size, especially with respect to timing of energy acquisition for breeding and frequency of breeding. Most endotherms are considered income breeders, meaning their reproductive expenditure (i.e. embryo nutrients and pregnancy maintenance) is fueled by simultaneous feeding (Bonnet *et al.*, 1998). Conversely, most temperate vipers (as well as many other viviparous snakes) are capital breeders (Bonnet *et al.*, 2001; and reviewed by Bonnet *et al.*, 1998; Shine, 2003, 2005). The reproductive expenditures of these species are fueled by energy and nutrients gained (and thus stored) at an earlier time (e.g. weeks, months, even years), rather than energy obtained during current feeding. There may be some plasticity within individuals and populations in the seasonal timing of follicular growth and in income and capital modes (i.e. Bonnet *et al.*, 2001; Lourdaux *et al.*, 2002; Taylor & DeNardo, 2005). Whether or not these patterns are “plastic” or genetically fixed in populations is unknown, and thus remain an important research question to address. In either event, vipers do not initiate follicle development until they have reached a species-specific threshold of fat reserves (Naulleau & Bonnet, 1996; Bonnet *et al.*, 2001).

While some females may take advantage of increased prey abundance and eat during earlier stages of gestation (Bonnet *et al.*, 2001; Taylor *et al.*, 2005; Ineich *et al.*, 2006; G.W. Schuett, unpublished data), traditionally, it was thought that any increase in metabolism in females during pregnancy (Ladyman *et al.*, 2003) would not result in increased energy transfer to embryos. There has been no documented maternal transfer of nutrients in vipers once embryonic growth begins (Ingermann, 1992; Bonnet *et al.*, 1998); however, given recent research in viviparous natricines providing anatomical evidence that embryos of gartersnakes (*Thamnophis*) acquire organic nutrients (e.g.

lipids, proteins) derived from the placenta (Blackburn & Lorenz, 2003a, b), it may be most parsimonious to assume that vipers may also have incipient placentotrophy. This hypothesis is perhaps supported by the findings of a lack of follicular growth in reproductive female western diamond-backed rattlesnakes from some Arizona populations until some time after emergence from hibernation (Taylor & DeNardo, 2005); however, this idea remains to be tested through detailed anatomical descriptions and experimentation.

Many populations of temperate vipers reproduce on a biennial (or less often) cycle (Fitch, 1960; Klauber, 1972; Schuett, 1992; Duvall, Arnold & Schuett, 1992; Forsman & Lindell, 1997; reviewed in Shine, 2003), although several studies have documented or hypothesized annual reproduction for female vipers, especially in warmer or richer environments (e.g. Wallace & Diller, 1990; Farrell, May & Pilgrim, 1995; Luiselli & Zuffi, 2002; Ineich *et al.*, 2006; Monteiro *et al.*, 2006). Some species may be physiologically capable of annual reproduction across their range, but achieve this potential only during very favourable conditions (Fitch & Pisani, 1993; Bonnet *et al.*, 2001; Taylor *et al.*, 2005). By contrast, an income breeding strategy permits many small mammalian endotherms to reproduce up to twice per year and for young to reproduce in their first year when prey densities are high (Mead & Wright, 1983; Korpimäki *et al.*, 1991; Jędrzejewski *et al.*, 1995), while larger mammals, e.g. Canada lynx, generally reproduce once per year but may increase litter size or juvenile survival when prey densities are high (Brand *et al.*, 1976; IUCN Cat Specialist Group, 2006; Logan & Sweanor, 2001).

Ectotherms have smaller neonate mass relative to maternal mass compared to similar-sized endotherms (Shine, 2005), so any increase in energetic output often occurs as additional offspring rather than increased investment in individual offspring (however, this pattern is variable and poorly understood; E. Taylor, personal communication). Litter size is variable among vipers, thus placing many species within the range of litter sizes for similar-sized endotherms, e.g. there can be 8–9 kits per litter for small mustelids (Mead & Wright, 1983), and 1–4 kittens per litter for Canada lynx (Brand *et al.*, 1976; G. Merrill, personal communication). Viper litter sizes range from 14 to 156 neonates per litter for subtropical to tropical species (e.g. Mexican west coast rattlesnake *C. basiliscus*, Klauber, 1972; puff adder *B. arietans*; Spawls & Branch, 1995), and three to 14 neonates per litter (averaging two to seven) for temperate vipers (Fitch, 1960; Klauber, 1972; Pomianowska-Pilipiuk, 1974; Bonnet *et al.*, 2001; Beaupre, 2002; Goldberg, 2002; Hill, 2004; Schuett *et al.*, 2005). Vipers do not exhibit periods of parental care of the young longer than the time for the occurrence of the first ecdysis, which is generally accomplished in 10 days or less after birth (Greene *et al.*, 2002; Reiserer, Schuett & Earley, 2007). This is in sharp contrast to most mammalian predators, which invest heavily in time and energy (e.g. nursing and lactation) in maternal care.

Vipers are relatively long-lived (some > 25 years; Brown, 1991; Greene, 1997; reviewed by Parker & Plummer, 1987), thus potentially increasing the lifetime reproductive capacity. However, in some cases (prey-poor environments and

extreme geographical limits), reproduction occurs at such long intervals that only one or two reproductive events occur during a female's lifetime regardless of longevity (Brown, 1991; Naulleau & Bonnet, 1996; Martin, 2002; Lourdaux *et al.*, 2002; Prival *et al.*, 2002; Hill, 2004).

Vipers also differ from similar-sized endotherms in adult longevity and per capita mortality. While difficult to quantify, mortality rates of individual vipers appear relatively low compared to those of similar-sized endotherms, especially for adults. Overwinter mortality rates ranging from 18% to 47% have been documented in vipers (reviewed by Parker & Plummer, 1987), with the highest rates seen in immature animals. There are few data on juvenile survivorship in vipers; however first-year survivorship in a limited few species of temperate vipers has been estimated to range from 12 to 77%. Survivorship in adults is better understood, and has been estimated at 69–95%, with an adult average of 77% (Fitch, 1960; Parker & Plummer, 1987; Brown, Kery & Hines, 2007). By contrast, small mustelids are characterized by relatively short life spans of one to two years (King, 1989). Annual adult survival estimates for larger mammalian predators are more often 50–70% (e.g. bobcat, Fuller *et al.*, 1995; coyote, Windberg, 1995), though species dependent on cyclic prey, e.g. Canada lynx, may have extremely high juvenile and adult survival during years of prey abundance (Poole, 1994).

V. PREDICTING VIPER FUNCTIONAL AND NUMERICAL RESPONSES

(1) Functional responses

Prey-dependent functional responses are most often calculated based on the Holling disk equation:

$$CN/(1 + ChN) \quad (1)$$

where C is the encounter rate with prey, h is the handling time of one prey item (during which other prey cannot be caught) and N is the prey population size (Abrams & Ginzburg, 2000).

Although handling time is often considered the time needed to subdue and engulf prey, the ability of vipers to eat extremely large prey relative to body mass, and the fact that large prey mass precludes foraging for a significant time afterwards during digestion, dictates that this extended digestive period should be included as part of 'h'. For example, individual least weasels may consume up to 20 voles per week (Jędrzejewska & Jędrzejewski, 1989; Table 2), while a western diamond-backed rattlesnake would be more likely to consume a maximum of one similar-sized rodent per week (Table 2). Likewise, vipers feeding on large prey, e.g. lagomorphs, would fall far below the potential maximum of one per day reported for Canada lynx feeding on snowshoe hare (Brand *et al.*, 1976; Table 2) due to the extended digestion period required by vipers (e.g. 0.07 lagomorphs per week, Table 2). The long digestive time of vipers might be considered functionally similar to large felid predators that feed exclusively on large kills for several

days (Mills & Biggs, 1993; Taber *et al.*, 1997; Logan & Sweanor, 2001; Carbone *et al.*, 2007). Overall, these comparisons suggest that handling time will be greater in vipers than in similar-sized mammalian predators, leading to overall lower functional responses and satiation at lower prey densities (Fig. 2).

Little is known about prey encounter rates (C) at differing prey densities for either endothermic or ectothermic terrestrial predators. Although vipers certainly employ some level of active searching, most are generally considered sit-and-wait predators, while most mammalian predators primarily employ active searching. As a result, overall encounter rates may be lower for vipers. Given that prey encounters by sit-and-wait or mobile ambushing predation could be viewed as random events of prey encountering relatively stationary predators (Taylor, 1984; Ivanov, 2004), the most parsimonious viper functional response curve might resemble a Type I linear functional response (Fig. 1A). Vipers may violate this assumption by using chemosensation to select ambush sites where prey or successful conspecifics have previously visited (Duvall *et al.*, 1990a; Ford & Burghardt, 1993; Roth *et al.*, 1999; Theodoratus & Chiszar, 2000; Clark, 2004, 2007); thus predation success may be affected by predator ratio-dependence (Abrams & Ginzburg, 2000). However, through experience and olfactory cues, certain prey species may learn to avoid sites chosen by vipers (Kotler, Blaustein & Brown, 1992; Kotler, Blaustein & Dednam, 1993; Kotler *et al.*, 2004; Jones, Mandelik & Dayan, 2001; Punzo, 2005) and thereby decrease encounter rates. Overall, there is little evidence that

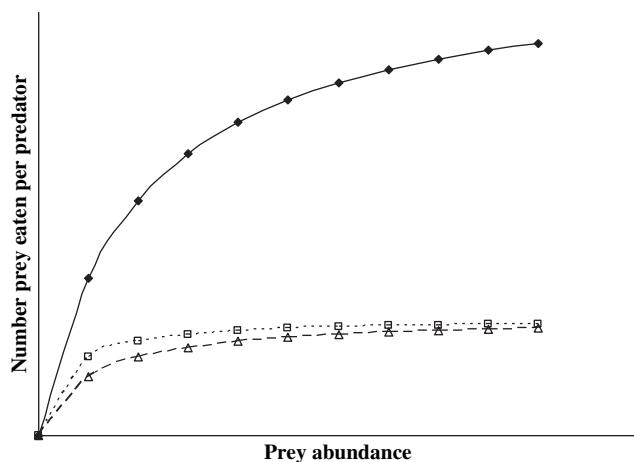


Fig. 2. Hypothetical Type I functional responses of a mammal predator (diamonds solid line) and a viper predator (dotted and dashed lines) assuming a handling time per prey item fourfold greater for vipers but similar encounter rates (open squares), or a handling time per prey item fourfold greater for vipers and attack rates half that of mammals due to either less active searching by vipers or because vipers' overlapping home ranges make them more likely to reduce prey encounters for each other (open triangles). Graph based on the equation $F = CN / (1 + ChN)$, where N = prey number, C = capture rate, h = handling time, and F = number of prey taken per predator (functional response).

vipers have encounter rates equal to or higher than similar-sized mammalian predators and, therefore, are unlikely to offset longer handling times with relatively greater encounter rates.

Although traditional views of functional responses considered a single predator responding to increasing prey density (as portrayed in Fig. 1), more recent models have argued that increasing predator density could alter functional responses (Abrams & Ginzburg, 2000). For example, increasing predator density could alter functional responses through increased competition or territoriality effects at higher predator densities (e.g. Capizzi & Luiselli, 1996; Taber *et al.*, 1997; Lode, 2000). Although many terrestrial endotherms defend resource-based territories from conspecifics and/or other species (e.g. mustelids; Sheffield & King, 1994; Lode, 2000; leopards, Henschel *et al.*, 2005; African lions, Hopcraft *et al.*, 2005), vipers have not been demonstrated to do so (Klauber, 1972; Bonnet *et al.*, 1998). Viper activity ranges frequently overlap both within and between viper species, as well as with other ectothermic predators (Beck, 1995; E.M. Nowak, G.W. Schuett, unpublished data). As a result, increasing predator density is more likely to affect vipers through reduced prey availability due to exploitative competition than through contest competition among vipers.

Lack of territoriality, in combination with low per-individual energy needs and tolerance of fasting, suggests that viper populations have the potential to become more dense than those of most mammalian predators, which could potentially increase the overall effect of vipers on prey populations (see Section V.3). Still, increasing viper density could alter functional responses in more subtle ways, such as removing that subset of the prey population that is especially vulnerable to snake predation (e.g. Swaisgood, Owings & Rowe, 1999) or fostering predator avoidance behaviours (Charnov, Orians & Hyatt, 1976).

Many vipers eat a variety of prey, so prey switching by adults is likely, especially for vipers that live in areas with rodent species with cyclic population fluctuations (e.g. Pomianowska-Pilipiuk, 1974; Forsman, 1991; Forsman & Lindell, 1997; after Erlinge *et al.*, 1983). The importance of alternative prey during cyclic mammal population declines has been demonstrated for mammalian and bird predators (Brand *et al.*, 1976; Todd *et al.*, 1981; Pech *et al.*, 1995; Kjellander & Nordström, 2003). Often predators feed selectively on the cyclic prey during periods of high density, but shift to include alternative prey during the low-density phase. Generalist predators, potentially including many vipers, could therefore have moderate to devastating consequences for less numerous or less preferred prey species when cyclic prey species enters a decline phase (e.g. Corbett & Newsome, 1987; Swihart *et al.*, 2001; Kent, Doncaster & Sluckin, 2003; Kjellander & Nordström, 2003; but see Prakash & de Roos, 2002). For vipers, the alternative prey are often smaller and more energetically costly to capture or consume than the primary prey (Arnold, 1993; Secor *et al.*, 1994; Shine & Sun, 2003; Ineich *et al.*, 2006). In some predators this forced switching to alternative prey causes a decline in predator recruitment (time-lapsed relative to primary prey decline; Brand *et al.*, 1976; Lawson *et al.*, 1998;

modeled by Oaten & Murdoch, 1975*b*; Schmitz, 1995; Belovsky *et al.*, 1989). In adult vipers, however, a decline in the abundance of the primary prey species may also be handled by fasting (Sun *et al.*, 2002). McCue (2007) has shown that adult western diamond-backed rattlesnakes have physiological adaptations for tolerating starvation in laboratory settings, which may mean that viper numerical responses may be less strongly tied to prey population cycles than those of endotherms. In some populations where reproduction may be based on long-term energy storage abilities (e.g. Bonnet *et al.*, 2001), viper populations could potentially maintain their populations during prey declines spanning one to three years. The plasticity of potential responses even within a species is exemplified by Forsman & Lindell (1997), who documented that survival of wild adders on one group of islands off the coast of Sweden increased with increased densities of field voles, yet was independent of field vole densities in another group of islands where the prey densities remained low between years.

Prey switching also might occur when individuals learn to specialize on unusual prey such as birds. In this case, learning will determine both the shape of the functional response as well as the energetic outcome of the encounter. Because birds can fly away after being envenomated by vipers, they may not leave the requisite chemical or heat trails normally used by vipers to track prey on the ground (e.g. Chiszar *et al.*, 1982; Theodoratus & Chiszar, 2000). Thus, most vipers that eat birds have evolved or learned the behavioural tendency to hold onto birds after striking in contrast to their usual strike-and-release predatory behaviour. Although many individual vipers have been known to eat birds occasionally (e.g. Fitch, 1960; Beavers, 1976; Wallace & Diller, 1990; Nowak & van Riper, 1999; Grismer, 2002; Prival *et al.*, 2002; M. Goode, D. Hardy, H. Greene & R. Howlett, personal communication), entire bird-eating populations of vipers are rare. Notable insular examples with morphological adaptations for ornithophagy (arboreal tendencies, longer fangs, longer tail, more anterior heart position, and longer head length) include the Chinese Shedao pit-viper (*Gloydius shedaoensis*; Shine & Sun, 2003; Shine *et al.*, 2003), and the Brazilian golden lancehead (*Bothrops insularis*; Martins *et al.*, 2002; Duarte & Garrubo, 2003; Wüster *et al.*, 2005). Given this potential for prey switching by vipers the functional response of many vipers is likely to follow a Type III curve (Fig. 1C).

(2) Numerical responses

The most common formula describing the numerical response is a simple linear one in which the numerical response is:

$$bg(N) - d \quad (2)$$

where b is the efficiency of converting food into offspring, g is the functional response at any given prey population size N , and d is *per capita* death rate (Abrams & Ginzburg, 2000). We argue above that vipers likely have lower functional responses than mammalian predators, so if conversion of prey to offspring and *per capita* mortality rates are otherwise similar, mammalian predators should have higher numerical responses (Fig. 3). However, the amount of energy

ectotherms can put towards reproduction is generally higher than that of endotherms due to the high energetic costs of endothermy itself (Bonnet *et al.*, 1998; Nagy, 2005; Shine, 2005), potentially increasing b in vipers compared to mammalian predators. Unfortunately, estimates of energy conversion to offspring are difficult to determine in wild vipers due to annual individual trade-offs in energy acquisition for breeding depending on available prey supply and female condition (Bonnet *et al.*, 1998, 2001; Lourdaix *et al.*, 2002; Shine, 2005). Likewise, adult vipers have relatively low *per capita* mortality rates, especially compared to small-bodied mustelid predators. As a result, if one assumes the *per capita* mortality rate of vipers is half that of similar-sized mammals and efficiency of prey conversion to offspring mirrors that estimated for overall net efficiency (least weasel averaged 2.3% net efficiency *versus* 41 to 49% for similar-sized syntopic adder (Pomianowska-Pilipiuk, 1974; Pough, 1980), then the numerical response of vipers could theoretically be greater than that of mammals like weasels (Fig. 3).

However, the potential for relatively strong numerical responses by wild vipers relative to mammalian predators of similar body size (mass) is likely largely constrained by the temporal pattern of reproduction in these snakes. The capital breeding exhibited by many vipers often results in reproduction in every other year, and reproductive response to increased prey abundance is expressed in the year after high prey densities, whereas income breeding small mammalian predators like weasels can respond more quickly to increases in prey abundance, either by increasing litter size, reproducing in the year they are born or having multiple litters. For example, in a recent study in which wild-living female western diamond-backed rattlesnakes were hand-fed

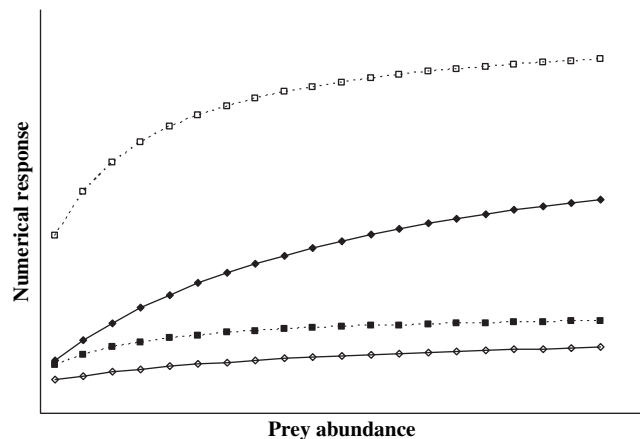


Fig. 3. Hypothetical numerical response of vipers (squares) and weasels (diamonds) based on functional responses shown in Fig. 2. If similar rates of prey conversion to offspring and similar *per capita* rates of mortality are assumed for weasels and vipers, the numerical response of weasels is higher (solid squares and diamonds). If vipers are assumed to have 40% energy conversion to offspring *versus* 2% for weasels and mortality rates of vipers are half those of weasels, then the numerical response of vipers is much greater (open squares and diamonds).

1-4 supplemental meals on a weekly basis, higher growth rates and post-parturient mass retention were documented in adult females, but an increase in litter or offspring size, which would have supported income breeding, was not documented (Taylor *et al.*, 2005). However, the potential for placentotrophy in vipers might allow for a faster numerical response to increased prey populations.

The available data suggest that the number of females achieving pregnancy, the number of young surviving in a litter, and post-parturient survival will likely increase the year following a pulse in prey density, but survival of the female and young (the inverse of d) will also depend on prey densities two years after the pulse (Forsman, 1991; Naulleau & Bonnet, 1996; Forsman & Lindell, 1997; Bonnet *et al.*, 2001; Lourdais *et al.*, 2002; Sun *et al.*, 2002; Gilg *et al.*, 2006). Unlike endotherms, most wild-living vipers do not eat during late gestation, resulting in predictable anorexia by the time the young are born, thus potentially compromising female survival post-birth (Bonnet *et al.*, 1998; Lourdais *et al.*, 2002; reviewed by Shine, 2003, 2005). Thus, increased prey populations would have to be maintained at least two years to sustain a numerical response by vipers, unless prey switching occurs.

(3) Total response: population regulation

Any regulatory effect of vipers is likely to be expressed at relatively low prey densities, given the relatively longer time required to transform prey energy into offspring compared to similar-sized endotherms. Given our hypothesized overall low functional response of individual vipers to changes in prey density (Fig. 2), driven primarily by lower energy requirements and long prey-processing times, if vipers regulate prey populations it will be through a numerical response (Fig. 3). We would not expect cyclical viper predator-prey oscillations of the magnitude of the classic mammalian predator-prey cycles seen at northern latitudes because of the slower time to respond to high prey abundances and the ability to fast during times of low prey abundance; this hypothesis is supported by fieldwork by Forsman & Lindell (1997). However, given the energy-efficient lifestyles of vipers, it should be theoretically possible to mount and maintain a numerical response at lower prey densities than for similar-sized endotherms (Fig. 3). The potential for a large population of low-energy, ectothermic predators to affect prey abundance has been demonstrated for other terrestrial ectothermic tetrapods, including coqui (*Eleutherodactylus coqui*; Stewart & Woolbright, 1996), multiple salamander species (Petranka & Murray, 2001), striped swamp snake (*Regina alleni*; Godley, 1980), brown tree snake (*B. irregularis*; Savidge, 1987; Rodda *et al.*, 1999) and hypothesized for snakes in general (Lillywhite, 1993; Parker & Plummer, 1987).

The energy-efficient lifestyle of vipers (including long-term fasting) may allow them to maintain relatively high population densities even when prey populations are low, thereby acting as a brake on the potential for prey populations to increase. Some species of vipers are locally very abundant. Typical densities range from 2-5 per ha in richer environments [e.g. habu *Protobothrops flavoviridis*

(Tanaka *et al.*, 1999); copperhead *Agkistrodon contortrix* (Fitch, 1960)]. We have estimated densities of western diamond-backed rattlesnakes at 0.14-15.5 per ha in the desert of central Arizona (E.M. Nowak, unpublished data). Sun *et al.*, (2001) estimated the density of Shedao pit-vipers to be 0.31 per linear meter of transect on Shedao Island, China! These estimated densities are roughly 100 to 1000-fold higher than those of mammalian predators like Canada lynx, 0.0002-0.001 per ha (3-13 per 130 km²; Brand *et al.*, 1976), and least weasel, 0.01 per ha (10 per 10 km²) during crash periods and 0.1 per ha (100 per 10 km²) in peak periods of vole cycles (Jędrzejewski *et al.*, 1995). In some cases, the differences in densities of mammalian and viper predators could offset the higher rate of prey consumption of endotherms, even when combined with the fact that in temperate areas endotherms remain active throughout the winter when vipers are hibernating. For example, weasels have been estimated to require one vole per day on average to meet their energy requirements (Gillingham, 1984) and are active throughout the year, although recorded kill rates are sometimes much higher at high rodent densities (2-4 per day) (Jędrzejewska & Jędrzejewski, 1989; Sundell *et al.*, 2000). As a result, a single weasel could kill between 365 and 1460 voles per year. By contrast, estimates suggest that temperate vipers take less than one similar-sized rodent prey per week (Table 2) and would do so for roughly 24 to 28 weeks per year for a total of less than 28 prey per snake per year. As a result, snake densities would have to be 10-100 times that of mammals like weasels to have similar effects on prey populations. The estimates of relative densities outlined above suggest this magnitude of difference may be achieved in some habitats. Perhaps most importantly, because of their low energy demands and ability to fast for long periods, vipers may be able to maintain relatively high densities when prey abundance is relatively low while endotherms would not. For example, both the rate of prey killing and the predator density of at least one mammalian predator (least weasel) has been shown to be tightly linked to rodent population cycles (Jędrzejewska & Jędrzejewski, 1989; Sundell *et al.*, 2000), a situation less likely for vipers due to capital breeding and low energy lifestyles.

Once prey populations escape any regulatory effect of vipers at low population sizes, *via* breeding during autumn, winter, or early spring when vipers are largely inactive, or by some other means, the relatively slow numerical response by vipers would be unlikely to bring the population into check again. For example, we estimated predation effects of adult male western diamond-backed rattlesnakes at two national monuments in central Arizona based on direct observations of predation on large prey (e.g. white-throated woodrat *Neotoma albigula*, and lagomorphs, primarily rabbits *Sylvilagus* sp.) during focal snake telemetric studies, mark-recapture studies of small mammals between 1994 and 2006, and scat analyses (E.M. Nowak, unpublished data.). Average annual predation rates for individual adult male western diamond-backed rattlesnakes at Montezuma Castle National Monument are estimated at 10.6 individual small (0.04 kg) prey (e.g. white-footed mice *Peromyscus* spp.) and 1.5 large (0.15-1.1 kg) prey (white-throated woodrats or

rabbits), or 1.48 individual small prey per ha and 0.21 large prey per ha (Table 2). Based on our estimates of snake and rodent densities, we calculate that in years with the highest rodent densities, western diamond-backed rattlesnakes could remove roughly 4% of the small prey population, and 3% of the woodrat population at this location. However, during years of low rodent densities, the same snakes could remove as many as 55% of the small prey and up to 60% of the woodrat population.

(4) Caveat: variation among vipers

Our discussion has focused primarily on temperate vipers, as these are one of the best known groups in terms diet and life-history traits. However, the patterns of numerical and functional responses we predict may not hold for other viper species (e.g. Ineich *et al.*, 2006). For example, many desert species rely on prey as a primary source of water for metabolism (Lillywhite, 1993; Beupre, 1996), with occasional unpredictable ambient moisture harvesting (e.g. Repp & Schuett, 2008). If prey population crashes occur, these animals may die from dehydration before they starve to death. For these populations and others, tapping energetic reserves to permit activity during cold temperatures to permit opportunistic feeding (Mori *et al.*, 2002) or moisture collection (Repp & Schuett, 2008) will necessitate long-term (efficient) energy storage. For tropical species inhabiting relatively stable climates, however, foraging strategies may be driven toward rapid energy acquisition and equally rapid conversion to growth and offspring (Martins *et al.*, 2002; Mori *et al.*, 2002; Ineich *et al.*, 2006), although there is a paucity of information on the basic biology of many tropical viper species.

VI. CONCLUSIONS

(1) The value of conceptual models like those of Holling's classical functional and numerical responses is that they permit researchers to define questions more precisely and offer novel hypotheses and predictions to guide future research. Our review suggests several ways in which the functional and numerical responses of vipers should differ from similar-sized endotherms, and testing the predictions and the assumptions upon which they are based would do much to expand our understanding of the role of vipers in predator-prey dynamics.

(2) The devastating impact of introduced brown tree-snakes on the native fauna of Pacific islands (Savidge, 1987) highlights the potential for snakes to significantly alter prey populations. The ecological impacts of recently introduced Burmese python (*Python molurus bivittatus*) in the Florida Everglades represent an on-going example of inadvertent introductions with unknown implications (Snow *et al.*, 2007). Previous systematic attempts to eradicate the habu, a large and potentially dangerous pitviper, on various heavily populated Japanese islands (reviewed in Rodda *et al.*, 1999) illustrate the often negative perceptions humans have

towards snakes, and towards venomous ones in particular. Studies are clearly necessary to understand the role of vipers in ecosystems, their potential for altering predator-prey dynamics when systems are perturbed, and their management and conservation.

(3) In light of the paucity of information about interactions of vipers and their prey, we suggest the following research avenues. First, the complexity of ecological interactions in many systems makes teasing apart fundamental population processes extremely difficult, and it is one of the reasons that the best studied predator-prey systems are relatively simple (e.g. lynx and hare, weasels and voles). As a result, the most productive initial studies of viper-prey interactions may be those in relatively simple island systems. A model for such studies is those of adders on islands in the Baltic where the primary prey (voles) and the interacting vertebrate community offered a relatively simple system to analyse (Forsman, 1991; Forsman & Lindell, 1997). Second, experimental manipulation is likely to be the most effective means for determining the potential for functional and numerical responses in vipers. Our predictions are based on assumptions derived primarily from field (natural history) observations. However, these may not accurately reflect the range of reproductive and/or behavioural responses that are possible, particularly if placentotrophy is validated in vipers. Last, comparative studies across viper taxa differing in prey types and life-history traits would be critical in understanding how life-history traits alter functional and numerical responses and the potential for prey population regulation. For example, hunting style, prey type and reproduction of temperate rattlesnakes and vipers likely contrast strongly with tropical species such as night adders (*Causus* spp.), a basal viperine (Ineich *et al.*, 2006), or members of the widely divergent Neotropical lanceheads (*Bothrops* spp.). Some members of the latter genus share features such as frequent consumption of small prey, slender body size, active foraging mode, and annual reproduction based on an income mode of energy acquisition (Martins *et al.*, 2002; see Ineich *et al.*, 2006), and thus would be good candidates for comparing both functional and numerical responses of vipers with strikingly different life-histories.

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VIII. REFERENCES

- ABRAMS, P. A. & GINZBURG, L. R. (2000). The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution* **15**, 337–341.
- ALBINO, A. M. (1993). Snakes from the Paleocene and Eocene of Patagonia (Argentina): paleoecology and coevolution with mammals. *Historical Biology* **7**, 51–69.
- ARNOLD, S. J. (1993). Foraging theory and prey-size – predator-size relations. In *Snakes: ecology and behavior* (eds. R. A. Seigel & J. T. Collins), pp. 87–115. McGraw-Hill, Inc., New York, NY.
- BEAUPRE, S. J. (1995a). Comparative ecology of the mottled rock rattlesnake, *Crotalus lepidus*, in Big Bend National Park. *Herpetologica* **15**, 45–56.
- BEAUPRE, S. J. (1995b). Effects of geographically variable thermal environment on bioenergetics of mottled rock rattlesnakes. *Ecology* **76**, 1655–1665.
- BEAUPRE, S. J. (1996). Field metabolic rate, water flux, and energy budgets of mottled rock rattlesnakes, *Crotalus lepidus*, from two populations. *Copeia* **1996**, 319–329.
- BEAUPRE, S. J. (2002). Modeling time-energy allocation in vipers: individual responses to environmental variation and implications for populations. In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas, & H. W. Greene), pp. 463–482. Eagle Mountain Publishing, Eagle Mountain, Utah.
- BEAUPRE, S. J. & ZAIDAN III, F. (2001). Scaling of CO₂ production in the timber rattlesnake (*Crotalus horridus*), with comments on cost of growth in neonates and comparative patterns. *Physiological and Biochemical Zoology* **74**, 757–768.
- BEAVERS, R. A. (1976). Food habits of the western diamondback rattlesnake, *Crotalus atrox*, in Texas. *The Southwestern Naturalist* **20**, 503–515.
- BECK, D. D. (1995). Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. *Journal of Herpetology* **29**, 211–223.
- BELOVSKY, G. E., RITCHIE, M. E. & MOORHEAD, J. (1989). Foraging in complex environments: when prey availability varies over time and space. *Theoretical Population Biology* **36**, 144–160.
- BLACKBURN, D. G., & LORENZ, R. L. (2003a). Placentation in garter snakes. II. Transmission EM of the chorioallantoic placenta of *Thamnophis radix* and *T. sirtalis*. *Journal of Morphology* **256**, 171–186.
- BLACKBURN, D. G., & LORENZ, R. L. (2003b). Placentation in garter snakes. III. Transmission EM of the omphalallantoic placenta of *Thamnophis radix* and *T. sirtalis*. *Journal of Morphology* **256**, 187–204.
- BONNET, X., BRADSHAW, D. & SHINE, R. (1998). Capital versus income breeding: an ectothermic perspective. *Oikos* **83**, 333–342.
- BONNET, X., NAULLEAU, G., SHINE, R. & LOURDAIS, O. (2001). Short-term versus long-term effects of food intake on reproductive output in a viviparous snake, *Vipera aspis*. *Oikos* **92**, 297–308.
- BOUTIN, S. (1995). Testing predator-prey theory by studying fluctuating populations of small mammals. *Wildlife Research* **22**, 89–100.
- BRAND, C. J., KEITH, L. B. & FISCHER, C. A. (1976). Lynx responses to changing snowshoe hare densities in central Alberta. *Journal of Wildlife Management* **40**, 416–428.
- BRISCHOUX, F., BONNET, X. & SHINE, R. (2007). Foraging ecology of sea kraits *Laticauda* spp. in the Neo-Caledonian Lagoon. *Marine Ecology Progress Series* **350**, 145–151.
- BROWN, J. H. & LASIEWSKI, R. C. (1972). Metabolism of weasels: The cost of being long and thin. *Ecology* **53**, 939–943.
- BROWN, W. S. (1991). Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. *Herpetologica* **47**, 101–115.
- BROWN, W. S. (1993). Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): A guide for conservation. *Society for the Study of Amphibians and Reptiles Herpetological Circular* **22**, Lawrence, Kansas.
- BROWN, W. S., KERY, M. & HINES, J. E. (2007). Survival of timber rattlesnakes (*Crotalus horridus*) estimated by capture-recapture models in relation to age, sex, color morph, time, and birthplace. *Copeia* **2007**, 656–671.
- CAPIZZI, D. & LUISELLI, L. (1996). Feeding relationships and competitive interactions between phylogenetically unrelated predators (owls and snakes). *Acta Oecologica* **17**, 265–284.
- CARBONE, C., TEACHER, A. & ROWCLIFFE, J. M. (2007). The costs of carnivory. *PLoS Biology* **5**, 0363–0368.
- CHALCRAFT, D. R. & RESETARITS, W. J. (2004). Metabolic rate models and the sustainability of predator populations. *Journal of Animal Ecology* **73**, 323–332.
- CHAPPELL, M. A. (1980). Thermal energetics and thermoregulatory costs of small arctic mammals. *Journal of Mammalogy* **61**, 278–291.
- CHARNOV, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9**, 129–136.
- CHARNOV, E. L., ORIAN, G. H. & HYATT, K. (1976). Ecological implications of resource depression. *American Naturalist* **110**, 247–259.
- CHISZAR, D., ANDREN, C., NILSON, G., O'CONNELL, B., MESTAS, J. S. JR., SMITH, H. W. & RADCLIFFE, C. W. (1982). Strike-induced chemosensory searching in Old World vipers and New World pit vipers. *Animal Learning and Behavior* **10**, 121–125.
- CLARK, R. W. (2002). Diet of the timber rattlesnake, *Crotalus horridus*. *Journal of Herpetology* **36**, 494–499.
- CLARK, R. W. (2004). Timber rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. *Journal of Chemical Ecology* **30**, 607–617.
- CLARK, R. W. (2006). Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. *Copeia* **2006**, 181–187.
- CLARK, R. W. (2007). Public information for solitary foragers: timber rattlesnakes use conspecific chemical cues to select ambush sites. *Behavioral Ecology* **18**, 487–490.
- COOPER, W. E. JR. (2005). The foraging mode controversy: both continuous variation and clustering of foraging movements occur. *Journal of the Zoology (London)* **267**, 179–190.
- COOPER, W. E. JR. (2007). Foraging modes as suites of coadapted movement traits. *Journal of Zoology (London)* **272**, 45–56.
- CORBETT, L. K. & NEWSOME, A. E. (1987). The feeding ecology of the dingo III. Dietary relationships with widely fluctuating prey populations in eastern Australia: an hypothesis of alteration of predation. *Oecologia* **7**, 215–227.

- CUNDALL, D. (2002). Envenomation strategies, head form, and feeding ecology in vipers. In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 149–162. Eagle Mountain Publishing, Eagle Mountain, Utah.
- DILLER, L. V. & JOHNSON, D. R. (1988). Food habits, consumption rates, and predation rates of western rattlesnakes and gopher snakes in southwestern Idaho. *Herpetologica* **44**, 228–233.
- DORCAS, M. E., HOPKINS, W. A. & ROE, J. H. (2004). Effects of body mass and temperature on standard metabolic rate in the eastern diamondback rattlesnake (*Crotalus adamanteus*). *Copeia* **2004**, 145–151.
- DOUGLAS, M. E., DOUGLAS, M. R., SCHUETT, G. W., PORRAS, L. W. & HOLYCROSS, A. T. (2002). Phylogeny of the western rattlesnake (*Crotalus viridis*) complex, with emphasis on the Colorado Plateau. In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 11–50. Eagle Mountain Publishing, Eagle Mountain, Utah.
- DUARTE, M. R. & GARRUBO, P. S. (2003). *Bothrops insularis* (golden lancehead). Diet. *Herpetological Review* **34**, 148.
- DUVALL, D., ARNOLD, S. J. & SCHUETT, G. W. (1992). Pitviper mating systems: ecological potential, sexual selection, and microevolution. In *Biology of the pitvipers* (eds. J. A. Campbell & E. D. Brodie, Jr.), pp. 321–336. Selva, Tyler, Texas.
- DUVALL, D., CHISZAR, D., HAYES, W. K., LEONHARDT, J. K. & GOODE, M. J. (1990 b). Chemical and behavioral ecology of foraging in prairie rattlesnakes (*Crotalus viridis viridis*). *Journal of Chemical Ecology* **16**, 87–101.
- DUVALL, D., GOODE, M. J., HAYES, W. K., LEONHARDT, J. K. & BROWN, D. G. (1990 a). Prairie rattlesnake vernal migration: field experimental analyses and survival value. *National Geographic Research* **6**, 457–469.
- DUVALL, D., KING, M. B. & GUTZWILLER, K. J. (1985). Behavioral ecology and ethology of the prairie rattlesnake. *National Geographic Research* **1**, 80–111.
- EIDE, N. E., EID, P. M., PRESTRUD, P. & SWENSON, J. E. (2005). Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape. *Wildlife Biology* **11**, 109–121.
- ERLINGE, S., GÖRANSSON, G., HANSSON, L., HÖGSTEDT, G., LIBERG, O., NILSSON, I. N., NILSSON, T., VON SCHANTZ, T., & SYLVÉN, M. (1983). Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos* **40**, 36–52.
- ERWIN, R. M. (1989). Predator-prey interactions, resource depression, and patch revisitation. *Behavioural Processes* **18**, 1–16.
- ESSINGTON, T. E. & HANSSON, S. (2004). Predator-dependent functional responses and interaction strengths in a natural food web. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 2215–2226.
- FARRELL, T. M., MAY, P. G. & PILGRIM, M. A. (1995). Reproduction in the rattlesnake, *Sistrurus miliarius barbouri*, in central Florida. *Journal of Herpetology* **29**, 21–27.
- FITCH, H. S. (1948). Ecology of the California ground squirrel on grazing lands. *American Midland Naturalist* **39**, 513–596.
- FITCH, H. S. (1960). Autecology of the copperhead. *University of Kansas Publication of the Museum of Natural History* **13**, 85–288.
- FITCH, H. S. (1970). Reproductive cycles of lizards and snakes. *University of Kansas Museum of Natural History Miscellaneous Publication* **52**, 1–247.
- FITCH, H. S. (1999). *A Kansas snake community: composition and change over 50 years*. Krieger Publishing, Malabar, Florida.
- FITCH, H. S. & PISANI, G. R. (1993). Life history traits of the western diamondback rattlesnake (*Crotalus atrox*) studied from roundup samples in Oklahoma. *Occasional Papers of the University of Kansas Museum of Natural History* **156**, 1–24.
- FORD, N. B. & BURGHARDT, G. M. (1993). Perceptual mechanisms and the behavioral ecology of snakes. In *Snakes: ecology and behavior* (eds. R. A. Seigel & J. T. Collins), pp. 117–164. McGraw-Hill Inc, New York.
- FORSMAN, A. (1991). Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *Journal of Animal Ecology* **60**, 253–267.
- FORSMAN, A. (1996). Body size and net energy gain in gape-limited predators: a model. *Journal of Herpetology* **30**, 307–319.
- FORSMAN, A. & LINDELL, L. E. (1997). Responses of a predator to variation in prey abundance: survival and emigration of adders in relation to vole density. *Canadian Journal of Zoology* **75**, 1099–1108.
- FRANZREB, K. E. (2007). Reproductive success and nest depredation of the Florida Scrub-jay. *Wilson Journal of Ornithology* **119**, 162–169.
- FRASER, W. R. & HOFMANN, E. E. (2003). A predator's perspective on the casual links between climate change, physical forcing, and ecosystem response. *Marine Ecology Progress Series* **265**, 1–15.
- FULLER, T. K., BERENDZEN, S. L., DECKER, T. A. & CARDOZA, J. E. (1995). Survival and cause-specific mortality rates of adult bobcats (*Lynx rufus*). *American Midland Naturalist* **134**, 404–408.
- GILG, O., SITTLER, B., SABARD, B., HURSTEL, A., SANÉ, R., DELATTRE, P. & HANSKI, I. (2006). Functional and numerical responses of four lemming predators in high Arctic Greenland. *Oikos* **113**, 193–216.
- GILLINGHAM, B. J. (1984). Meal size and feeding rate in the least weasel *Mustela nivalis*. *Journal of Mammalogy* **65**, 517–519.
- GODLEY, J. S. (1980). Foraging ecology of the striped swamp snake, *Regina alleni*, in southern Florida. *Ecological Monographs* **50**, 411–436.
- GOLDBERG, S. R. (2002). Reproduction in the Arizona black rattlesnake, *Crotalus viridis cerberus* (Viperidae). *Herpetological Natural History* **9**, 75–78.
- GOLLEY, F. B., PETRIDES, G. A., RAUBER, E. L. & JENKINS, J. H. (1965). Food intake and assimilation by bobcats under laboratory conditions. *Journal of Wildlife Management* **29**, 442–447.
- GREENE, H. W. (1983). Dietary correlates of the origin and radiation of snakes. *American Zoologist* **23**, 431–441.
- GREENE, H. W. (1986). Natural history and evolutionary biology. In *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates* (eds. M. E. Feder & G. V. Lauder), pp. 99–108. The University of Chicago Press, Chicago, Illinois.
- GREENE, H. W. (1992). The ecological and behavioral context for pitviper evolution. In *Biology of the pitvipers* (eds. J. A. Campbell & E. D. Brodie, Jr.), pp. 107–117. Selva, Tyler, Texas.
- GREENE, H. W. (1997). *Snakes: the evolution of mystery in nature*. University of California Press, Berkeley, California.
- GREENE, H. W., MAY, P. G., HARDY, D. L. Sr., SCITURRO, J. M. & FARRELL, T. M. (2002). Parental behavior by vipers. In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 177–206. Eagle Mountain Publishing, Eagle Mountain, Utah.
- GRISMER, L. L. (2002). *Amphibians and reptiles of Baja California*. University of California Press, Berkeley, California.
- HANSKI, I. & HENTTONEN, H. (1996). Predation on competing vole species: a simple explanation of complex patterns. *Journal of Animal Ecology* **65**, 220–232.
- HENSCHER, P., ABERNETHY, K. A. & WHITE, L. J. T. (2005). Leopard food habits in the Lopè National Park, Gabon, Central Africa. *African Journal of Ecology* **43**, 21–28.
- HILL, J. G. III. (2004). Natural history of the western cottonmouth (*Agkistrodon piscivorus leucostoma*) from an upland lotic population

- in the Ozark Mountains of Northwest Arkansas. *Unpublished Dissertation*, University of Arkansas, Fayetteville.
- HIMES, J. G. (2002). The role of the midland water snake, *Nerodia sipedon* (Serpentes: Colubridae), as a predator: foraging behavior, kin recognition, and the response of prey. *Amphibia-Reptilia* **23**, 333–342.
- HOLLING, C. S. (1959 *a*). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *The Canadian Entomologist* **91**, 293–320.
- HOLLING, C. S. (1959 *b*). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* **91**, 385–398.
- HOLYCROSS, A. T., PAINTER, C. W., BARKER, D. G. & DOUGLAS, M. E. (2002). Foraging ecology of the threatened ridge-nosed rattlesnake (*Crotalus willardi obscurus*). In *Biology of the pitvipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 243–252. Eagle Mountain Publishing, Eagle Mountain, Utah.
- HOPCRAFT, J. G. C., SINCLAIR, A. R. E. & PACKER, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology* **74**, 559–566.
- INEICH, I., BONNET, X., SHINE, R., SHINE, T., BRISCHOUX, F., LEBRETON, M. & CHIRIO, L. (2006). What, if anything, is a 'typical' viper? Biological attributes of basal viperid snakes (genus *Causus* Wagler, 1830). *Biological Journal of the Linnean Society* **89**, 575–588.
- INGERMANN, R. L. (1992). Maternal-fetal oxygen transfer in lower vertebrates. *American Zoologist* **32**, 322–331.
- IUCN CAT SPECIALIST GROUP (2006). Cat species information. In: IUCN 2006. 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 10 February 2007.
- IVANOV, V. K. (2004). Specific features of the functional response of a sluggish predator to mobile prey in an aquatic environment (experimental approach). *Russian Journal of Ecology* **35**, 354–356.
- JĘDRZEJSKA, B. & JĘDRZEJSKI, W. (1989). Seasonal surplus killing as a hunting strategy of the weasel *Mustela nivalis* - test of a hypothesis. *Acta Theriologica* **34**, 347–359.
- JĘDRZEJSKI, W., JĘDRZEJSKA, B. & SZYMURA, L. (1995). Weasel population response, home range, and predation on rodents in a deciduous forest in Poland. *Ecology* **76**, 179–195.
- JEPSEN, J. U., EIDE, N. E., PRESTRUD, P. & JACOBSEN, L. B. (2002). The importance of prey distribution in habitat use by arctic foxes (*Alopex lagopus*). *Canadian Journal of Zoology* **80**, 418–429.
- JOHNSON, D. W. (2006). Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. *Ecology* **87**, 1179–1188.
- JONES, M., MANDELIK, Y. & DAYAN, T. (2001). Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behavior. *Ecology* **82**, 2164–2176.
- KEITH, L. B., TODD, A. W., BRAND, C. J., ADAMCIK, R. S. & RUSCH, D. H. (1977). An analysis of predation during a cyclic fluctuation of snowshoe hares. *Proceedings of the International Congress of Game Biologists*, 151–175.
- KENT, A., DONCASTER, C. P. & SLUCKIN, T. (2003). Consequences for predators of rescue and Allee effects on prey. *Ecological Modelling* **162**, 233–245.
- KING, C. (1989). *The natural history of weasels and stoats*. Christopher Helm, London.
- KISSUI, B. M. & PACKER, C. (2004). Top-down population regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society B* **271**, 1867–1874.
- KJELLANDER, P. & NORDSTRÖM, J. (2003). Cyclic voles, prey switching in red fox, and roe deer dynamics - a test of the alternative prey hypothesis. *Oikos* **101**, 338–344.
- KLAUBER, L. M. (1972). *Rattlesnakes: their habits, life histories, and influence on mankind*. Two volumes, 2nd edition. University of California Press, Berkeley, California.
- KORPIMÄKI, E. & NORRDAHL, K. (1991). Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecology* **72**, 814–826.
- KORPIMÄKI, E., NORRDAHL, K. & RINTA-JASKARI, T. (1991). Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia* **88**, 552–561.
- KOTLER, B. P., BLAUSTEIN, L. & BROWN, J. S. (1992). Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Annals of Zoology Fennici* **29**, 199–206.
- KOTLER, B. P., BLAUSTEIN, L. & DEDNAM, H. (1993). The *specter* of predation: the effects of vipers on the foraging behavior of two gerbilline rodents. *Israel Journal of Zoology* **39**, 11–21.
- KOTLER, B. P., BROWN, J. S., BOUSKILA, A., MUKHERJEE, S. & GOLDBERG, T. (2004). Foraging games between gerbils and their predators: seasonal changes in schedules of activity and apprehension. *Israel Journal of Zoology* **50**, 255–271.
- KŘIVAN, V. & VRKOČ, I. (2004). Should "handled" prey be considered? Some consequences for functional response, predator-prey dynamics and optimal foraging theory. *Journal of Theoretical Biology* **227**, 167–174.
- LADYMAN, M., BONNET, X., LOURDAIS, O., BRADSHAW, D. & NAULLEAU, G. (2003). Gestation, thermoregulation, and metabolism in a viviparous snake, *Vipera aspis*: evidence for fecundity-independent costs. *Physiological and Biochemical Zoology* **76**, 497–510.
- LAUNDRE, J. W. & HERNANDEZ, L. (2003). Total energy budget and prey requirements of free-ranging coyotes in the Great Basin Desert of the western United States. *Journal of Arid Environments* **55**, 675–689.
- LAWSON, J. W., ANDERSON, J. T., DALLEY, E. L. & STENSON, G. B. (1998). Selective foraging by harp seals *Phoca groenlandica* in nearshore and offshore waters of Newfoundland, 1993 and 1994. *Marine Ecology Progress Series* **163**, 1–10.
- LILLYWHITE, H. B. (1993). Temperature, energetics, and physiological ecology. In *Snakes: ecology and evolutionary biology* (eds. R. A. Seigel, J. T. Collins & S. S. Novak), pp. 422–477. (reprint of first edition). The Blackburn Press, USA.
- LILLYWHITE, H. B., DE DELVA, P. & NOONAN, B. P. (2002). Patterns of gut passage time and chronic retention of fecal mass in viperid snakes. In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 497–506. Eagle Mountain Publishing, Eagle Mountain, Utah.
- LODE, T. (2000). Functional response and area-restricted search in a predator: seasonal exploitation of anurans by the European polecat, *Mustela putorius*. *Animal Ecology* **25**, 223–231.
- LOGAN, K. A. & SWEANOR, L. L. (2001). *Desert puma: evolutionary ecology and conservation of an enduring carnivore*. Island Press, Washington, District of Columbia.
- LOURDAIS, O., BONNET, X., SHINE, R., DENARDO, D., NAULLEAU, G. & GUILLON, M. (2002). Capital-breeding and reproductive effort in a variable environment: a longitudinal study of a viviparous snake. *Journal of Animal Ecology* **71**, 470–479.
- LUISELLI, L. & ZUFFI, M. A. (2002). Female life history traits of the asp viper (*Vipera aspis*) and sand viper (*V. ammodytes*) from the Mediterranean region. In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 279–382. Eagle Mountain Publishing, Eagle Mountain, Utah.
- MACARTHUR, R. H. & PIANKA, E. R. (1966). On optimal use of a patchy environment. *American Naturalist* **100**, 603–609.

- MACARTNEY, J. M., GREGORY, P. T. & CHARLAND, M. B. (1990). Growth and sexual maturity of the western rattlesnake, *Crotalus viridis*, in British Columbia. *Copeia* **1990**, 528–524.
- MACARTNEY, J. M., GREGORY, P. T., & LARSEN, K. W. (1988). A tabular survey of data on movements and home ranges of snakes. *Journal of Herpetology* **22**, 61–73.
- MARCELLI, M., FUSILLO, R. & BOITANI, L. (2003). Sexual segregation in the activity patterns of European polecats. *Journal of Zoology (London)* **261**, 249–255.
- MARTIN, W. H. (2002). Life history constraints on the timber rattlesnake (*Crotalus horridus*) at its climatic limits. In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 285–306. Eagle Mountain Publishing, Eagle Mountain, Utah.
- MARTINS, M. M., MARQUES, O. A. V. & SAZIMA, I. (2002). Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops*. In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 307–328. Eagle Mountain Publishing, Eagle Mountain, Utah.
- MAY, R. M. (1988). How many species are there on earth? *Science* **241**, 1441–1449.
- MCCUE, M. D. (2007). Western diamondback rattlesnakes demonstrate physiological and biochemical strategies for tolerating prolonged starvation. *Physiological and Biochemical Zoology* **80**, 25–34.
- MEAD, R. A. & WRIGHT, P. L. (1983). Reproductive cycles of Mustelidae. *Acta Zoologica Fennica* **174**, 169–172.
- MESSIER, F. (1994). Ungulate population models with predation: a case study with the North American moose. *Ecology* **75**, 478–488.
- MILLS, M. G. L. & BIGGS, H. C. (1993). Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Symposium of the Zoological Society of London* **65**, 253–268.
- MILLS, M. G. L. & SHENK, T. M. (1992). Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *Journal of Animal Ecology* **61**, 693–702.
- MIZUTANI, F. & JEWELL, P. A. (1998). Home-range and movements of leopards (*Panthera pardus*) on a livestock ranch in Kenya. *Journal of Zoology (London)* **244**, 269–286.
- MONTEIRO, C., MONTGOMERY, C. E., SPINA, F., SAWAYA, R. C. & MARTINS, M. (2006). Feeding, reproduction, and morphology of *Bothrops matrogrossensis* (Serpentes, Viperidae, Crotalinae) in the Brazilian Pantanal. *Journal of Herpetology* **40**, 408–413.
- MORI, A., TODA, M. & OTA, H. (2002). Winter activity of the himehabu (*Ovophis okinawensis*) in the humid subtropics: Foraging on breeding anurans at low temperatures. In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 329–344. Eagle Mountain Publishing, Eagle Mountain, Utah.
- NAGY, K. A. (2005). Field metabolic rate and body size. *Journal of Experimental Biology* **208**, 1621–1625.
- NAULLEAU, G. & BONNET, X. (1996). Body condition threshold for breeding in a viviparous snake. *Oecologia* **107**, 301–306.
- NOWAK, E. M. (2005). Movement patterns and life history of western diamond-backed rattlesnakes (*Crotalus atrox*) at Tuzigoot National Monument, Arizona. In *Proceedings of the 7th biennial conference of research on the Colorado Plateau* (eds. C. van Riper III & D. Mattson), pp. 253–274. University of Arizona Press, Tucson, Arizona.
- NOWAK, E. M., HARE, T. & McNALLY, J. (2002). Management of “nuisance” vipers: effects of translocation on western diamondback rattlesnakes (*Crotalus atrox*). In *Biology of the vipers* (eds. G. W. Schuett, M. Höggren, M. E. Douglas & H. W. Greene), pp. 533–560. Eagle Mountain Publishing, Eagle Mountain, Utah.
- NOWAK, E. M. & VAN RIPER III, C. (1999). Effects and effectiveness of rattlesnake relocation at Montezuma Castle National Monument. U.S. Geological Survey/FRESC Report Series USGS/FRESC/COPL/1999/17.
- OATEN, A. & MURDOCH, W. W. (1975 *a*). Functional response and stability in predator-prey systems. *American Naturalist* **109**, 289–298.
- OATEN, A. & MURDOCH, W. W. (1975 *b*). Switching, functional response and stability in predator-prey systems. *American Naturalist* **109**, 299–318.
- OVERHOLTZER-MCLEOD, K. L. (2006). Consequences of patch reef spacing for density-dependent mortality of coral-reef fishes. *Ecology* **87**, 1017–1026.
- PARKER, W. S. & PLUMMER, M. V. (1987). Population ecology. In *Snakes: ecology and evolutionary biology* (eds. R. A. Seigel, J. T. Collins & S. S. Novak), pp. 253–301. Macmillan, New York.
- PECH, R. P., SINCLAIR, A. R. E. & NEWSOME, A. E. (1995). Predation models for primary and secondary prey species. *Wildlife Research* **22**, 55–64.
- PECH, R. P., SINCLAIR, A. R. E., NEWSOME, A. E. & CATLING, P. C. (1992). Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. *Oecologia* **89**, 102–112.
- PETRANKA, J. W. & MURRAY, S. S. (2001). Effectiveness of removal sampling for determining salamander density and biomass: a case study in an Appalachian streamside community. *Journal of Herpetology* **35**, 36–44.
- PITT, W. C. & RITCHIE, M. E. (2002). Influence of prey distribution on the functional response of lizards. *Oikos* **96**, 157–163.
- POMIANOWSKA-PILPIUK, I. (1974). Energy balance and food requirements of adult vipers (*Vipera berus*). *Ekologia Polska* **22**, 195–211.
- POOLE, K. G. (1994). Characteristics of an unharvested lynx population during a snowshoe hare decline. *Journal of Wildlife Management* **58**, 608–618.
- POUGH, F. H. (1980). The advantages of ectothermy for tetrapods. *American Naturalist* **115**, 92–112.
- POUGH, F. H. & GROVES, J. D. (1983). Specializations of the body form and food habits of snakes. *American Zoologist* **23**, 443–454.
- PRAKASH, S. & DE ROOS, A. M. (2002). Habitat destruction in a simple predator-prey patch model: how predators enhance prey persistence and abundance. *Theoretical Population Biology* **62**, 231–249.
- PRIVAL, D. B., GOODE, M. J., SWANN, D. E., SCHWALBE, C. R. & SCHROFF, M. J. (2002). Natural history of a northern population of twin-spotted rattlesnakes, *Crotalus pricei*. *Journal of Herpetology* **36**, 598–607.
- PUNZO, F. (2005). Chemosensory recognition by males of the desert pocket mouse, *Chaetodipus penicillatus*, to odors of various species of snakes. *Ethology, Ecology and Evolution* **17**, 83–89.
- RADLOFF, F. G. T., & DU TOIT, J. T. (2004). Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology* **73**, 410–423.
- REICHENBACH, N. G., & DALRYMPLE, G. H. (1986). Energy use, life histories, and the evaluation of potential competition in two species of garter snake. *Journal of Herpetology* **20**, 133–153.
- REISERER, R. S., SCHUETT, G. W. & EARLEY, R. L. (2007). Dynamic aggregations of newborn sibling rattlesnakes exhibit stable thermoregulatory properties. *Journal of Zoology* **274**, 277–283.
- REPR, R. A. & SCHUETT, G. W. (2008). Adult western diamond-backed-rattlesnakes, *Crotalus atrox* (Serpentes: Viperidae) gain

- water by harvesting and drinking rain, sleet and snow. *The Southwestern Naturalist* **53**, 108–114.
- RITCHIE, M. E. (1998). Scale-dependent foraging and patch choice in fractal environments. *Evolutionary Ecology* **12**, 309–330.
- RODDA, G. H., SAWAI, Y., CHISZAR, D. & TANAKA, H. (1999). *Problem snake management: the habu and the brown treesnake*. Cornell University Press, Ithaca, NY.
- ROTH, E. D. & JOHNSON, J. A. (2004). Size-based variation in antipredator behavior within a snake (*Agkistrodon piscivorus*) population. *Behavioral Ecology* **15**, 365–370.
- ROTH, E. D., MAY, P. G., & FARRELL, T. M. (1999). Pigmy rattlesnakes use frog-derived chemical cues to select foraging sites. *Copeia* **1999**, 772–774.
- SABO, J. L. & POWER, M. E. (2002). Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. *Ecology* **83**, 3023–3036.
- SAVIDGE, J. A. (1987). Extinction of an island forest avifauna by an introduced snake. *Ecology* **68**, 660–668.
- SCHMITZ, O. (1995). Functional responses of optimal consumers and the potential for regulation of resource populations. *Wildlife Research* **22**, 101–113.
- SCHUETT, G. W. (1992). Is long-term sperm storage an important component of the reproductive biology of temperate pitvipers? In *Biology of the pitvipers* (eds J. A. Campbell & E. D. Brodie, Jr.), pp. 169–184. Selva, Tyler, Texas.
- SCHUETT, G. W., HARDY, S. D. L., GREENE, H. W., EARLEY, R. L., GROBER, M. S., VAN KIRK, E. A. & MURDOCH, W. J. (2005). Sympatric rattlesnakes with contrasting mating systems show differences in seasonal patterns of plasma sex steroids. *Animal Behaviour* **70**, 257–266.
- SCHUETT, G. W., NOWAK, E. M. & REPP, R. A. (2002). *Crotalus cerberus*: diet and prey size. *Herpetological Review* **33**, 210–211.
- SECOR, S. M., & DIAMOND, J. (2000). Evolution of regulatory responses to feeding in snakes. *Physiological & Biochemical Zoology* **73**, 123–142.
- SECOR, S. M. & NAGY, K. A. (1994). Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* **75**, 1600–1614.
- SECOR, S. M., STEIN, E. D. & DIAMOND, J. (1994). Rapid upregulation of snake intestine in response to feeding: a new model of intestinal adaptation. *American Journal of Physiology* **266**, G695–G705.
- SHEFFIELD, S. R. & KING, C. M. (1994). *Mustela nivalis*. *Mammalian Species* **454**, 1–10.
- SHINE, R. (2003). Reproductive strategies in snakes. *Proceedings of the Royal Society B* **270**, 995–1004.
- SHINE, R. (2005). Life-history evolution in reptiles. *Annual Review of Ecology, Evolution, and Systematics* **36**, 23–46.
- SHINE, R. & BONNET, X. (2000). Snakes: a new 'model organism' in ecological research? *Trends in Ecology & Evolution* **15**, 221–222.
- SHINE, R., FITZGERALD, M. & KEARNEY, M. (2003). A radiotelemetric study of movements and thermal biology of insular Chinese pit-vipers (*Gloydus shedaoensis*, Viperidae). *Oikos* **100**, 342–352.
- SHINE, R. & SUN, L.-X. (2003). Attack strategy of an ambush predator: Which attributes of the prey trigger a pit-viper's strike? *Functional Ecology* **17**, 340–348.
- SNOW, R. W., KRYSKO, K. L., ENGE, K. M., OBERHOFER, L., WARREN-BRADLEY, A. & WILKINS, L. (2007). Introduced populations of *Boa constrictor* (Boidae) and *Python molurus bivittatus* (Pythonidae) in southern Florida. In *Biology of the boas and pythons* (eds R. W. Henderson & R. Powell), pp. 417–438. Eagle Mountain Publishing, Eagle Mountain, Utah.
- SOLOMON, M. E. (1949). The natural control of animal populations. *Journal of Animal Ecology* **18**, 1–35.
- SPAULS, S. & BRANCH, B. (1995). *The dangerous snakes of Africa*, p. 116. Ralph Curtis Books, Sanibel Island, Florida.
- SPONG, G. (2002). Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. *Behavioral Ecology and Sociobiology* **52**, 303–307.
- SPOTILA, J. R. & STANDORA, E. A. (1985). Energy budgets of ectothermic vertebrates. *American Zoologist* **25**, 973–986.
- STEWART, M. M. & WOOLBRIGHT, L. L. (1996). Amphibians. In *The food web of a tropical rainforest* (eds D. P. Reagan & R. B. Waide), pp. 273–320. The University of Chicago Press, Chicago, Illinois.
- STROMBERG, M., RAYBURN, R. L. & CLARK, T. W. (1983). Black-footed ferret prey requirements: an energy balance estimate. *Journal of Wildlife Management* **47**, 67–73.
- SUN, L.-X., SHINE, R., DEBI, Z. & ZHENGREN, T. (2001). Biotic and abiotic influences on activity patterns of insular pit-vipers (*Gloydus shedaoensis*, Viperidae) from northeastern China. *Biological Conservation* **97**, 387–398.
- SUN, L.-X., SHINE, R., DEBI, Z. & ZHENGREN, T. (2002). Low costs, high output: reproduction in an insular pit-viper (*Gloydus shedaoensis*, Viperidae) from northeastern China. *Journal of Zoology (London)* **256**, 511–521.
- SUNDELL, J., NORRDAHL, K., KORPIMÄKI, E. & HANSKI, I. (2000). Functional response of the least weasel *Mustela nivalis nivalis*. *Oikos* **90**, 501–508.
- SWAISGOOD, R. R., OWINGS, D. H. & ROWE, M. P. (1999). Conflict and assessment in a predator-prey system: ground squirrels versus rattlesnakes. *Animal Behaviour* **57**, 1033–1044.
- SWIHART, R. K., FENG, Z., SLADE, N. A., MASON, D. M. & GEHRING, T. G. (2001). Effects of habitat destruction and resource supplementation in a predator-prey metapopulation model. *Journal of Theoretical Biology* **210**, 287–303.
- TABER, A. B., NOVARO, A. J., NERIS, N. & COLMAN, F. H. (1997). The food habits of sympatric jaguar and puma in the Paraguayan Chaco. *Biotropica* **29**, 204–213.
- TANAKA, H., HAYASHI, Y. & WADA, Y. (1999). Population density of habu on the Armani Islands, as estimated by removal methods. In *Problem snake management: the habu and the brown treesnake* (eds G. H. Rodda, Y. Sawai, D. Chiszar & H. Tanaka), pp. 230–235. Cornell University Press, Ithaca, New York.
- TAYLOR, E. N. & DENARDO, D. F. (2005). Sexual size dimorphism and growth plasticity in snakes: an experiment on the western diamond-backed rattlesnake (*Crotalus atrox*). *Journal of Experimental Zoology Part A: Comparative Experimental Biology* **303A**, 7598–7607.
- TAYLOR, E. N., MALAWY, M. A., BROWNING, D. M., LEMAR, S. V. & DENARDO, D. F. (2005). Effects of food supplementation on the physiological ecology of female western diamond-backed rattlesnakes (*Crotalus atrox*). *Oecologia* **144**, 206–213.
- TAYLOR, R. J. (1984). The functional response: the influence of predatory behavior upon dynamics. In *Predation*. (ed. R. J. Taylor), pp. 82–100. Chapman and Hall, New York.
- THEODORATUS, D. H. & CHISZAR, D. (2000). Habitat selection and prey odor in the foraging behavior of western rattlesnakes (*Crotalus viridis*). *Behaviour* **137**, 119–135.
- TINBERGEN, L. (1960). The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. *Archives Néerlandaises de Zoologie* **13**, 266–336.
- TODD, A. W., KEITH, L. B. & FISCHER, D. A. (1981). Population ecology of coyotes during a fluctuation of snowshoe hares. *Journal of Wildlife Management* **45**, 629–640.

- VUCETICH, J. A., PETERSON, R. O. & SCHAEFER, C. L. (2002). The effect of prey and predator densities on wolf predation. *Ecology* **83**, 3003–3013.
- WALLACE, R. L. & DILLER, L. V. (1990). Feeding ecology of the rattlesnake, *Crotalus viridis oreganus*, in northern Idaho. *Journal of Herpetology* **24**, 246–253.
- WINDBERG, L. A. (1995). Demography of a high-density coyote population. *Canadian Journal of Zoology* **73**, 942–954.
- WÜSTER, W., DUARTE, M. R. & DA GRAÇA SALOMÃO, M. (2005). Morphological correlates of incipient arboreality and ornithophagy in island pitvipers, and the phylogenetic position of *Bothrops insularis*. *Journal of Zoology* **266**, 1–10.