

# Individual Variability: The Missing Component to Our Understanding of Predator–Prey Interactions

Nathalie Pettorelli<sup>\*,†</sup>, Anne Hilborn<sup>\*,†</sup>, Clare Duncan<sup>\*,‡</sup>,  
Sarah M. Durant<sup>\*</sup>

<sup>\*</sup>Institute of Zoology, Zoological Society of London, London, United Kingdom

<sup>†</sup>Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, Virginia, USA

<sup>‡</sup>UCL Department of Geography, University College London, London, United Kingdom

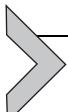
<sup>1</sup>Corresponding author: e-mail address: nathalie.pettorelli@ioz.ac.uk

## Contents

1. Introduction	20
2. What Shapes Predation Risk and Prey Selection?	23
2.1 Predation risk	23
2.2 Prey selection	25
3. Individual Variability and Functional Responses	28
3.1 Impact on the strength of the response	28
3.2 Impact on the type of response	29
4. Accounting for Individual Variability When Modelling Predator–Prey Interactions	30
5. Conclusions	35
Appendix	37
References	38

## Abstract

Predator–prey interactions are central to our understanding of adaptive evolution and community ecology. A growing body of research indicates that predation risk and prey selection can be highly variable from one individual to another; nonetheless, individual variability both within predators and within prey is still classically ignored when attempting to model predator–prey dynamics. This chapter explores how our current knowledge of the factors shaping prey selection and predation risk relate to current modelling approaches of predator–prey dynamics. It also discusses how dismissal of inherent individual heterogeneity in predator–prey interactions may be impacting our ability to advance food web theory as well as our understanding of evolutionary trajectories in predator and prey populations. It finally reviews possible methodological frameworks that could help integrate individual variability into the modelling of predator–prey interactions.



## 1. INTRODUCTION

Interactions, should they be among organisms or between abiotic environmental conditions and organisms, define the processes that shape the diversity of life on Earth at both the ecological and the evolutionary scales. Predator–prey interactions, in particular, are powerful forces that underpin the behaviour and ecology of all organisms (Arditi and Ginzburg, 2012; Drossel et al., 2004), being at the heart of our understanding of adaptive evolution (Mousseau et al., 2000). Predation can indeed change the distribution of life history traits over generations and influence prey evolution, through prey selectivity, the direct induction of traits and the indirect induction of traits via reduced or increased competition (Relyea, 2002; Reznick et al., 1990; Wittmer et al., 2005). Moreover, predation may increase stability in trophic interactions, and the exertion of top-down control from secondary consumers is a crucial link in structuring ecological communities (Hairston et al., 1960; May, 1973; Ripple et al., 2014; Yeakel et al., 2014). A large part of our ability to explain how biodiversity is distributed, how communities are structured and how ecosystems function is thus directly linked to our ability to decipher predator–prey interactions (Litvaitis, 2000).

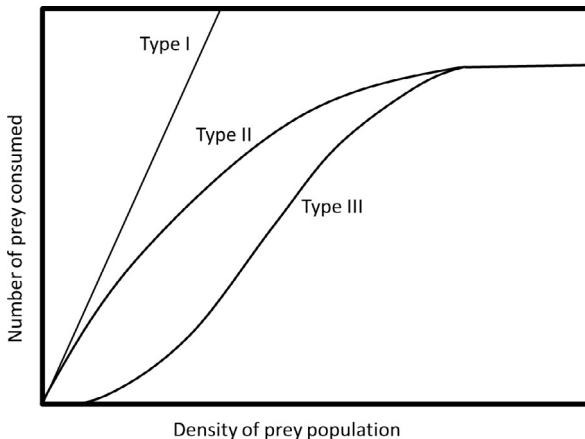
Central to theories underpinning our current understanding of predator–prey interactions are the concepts of predation risk, prey selection, numerical response and functional response. Predation risk refers to an individual's propensity to be predated upon by another organism. This risk can compromise an organism's ability to acquire and maintain body reserves by hindering foraging time and efficiency and increasing physiological stress (Creel and Christianson, 2008), making it a key determinant of energy intake per unit time and individual fitness. To avoid being predated, organisms can indeed modify their habitat selection patterns (Gilliam and Fraser, 1987) and change trophic flows by altering the selection of their diet (Schmitz, 1998); such anti-predator tactics can lead to prey reducing their energy intake, and/or prey increasing their energetic allocation to predator avoidance strategies. These shifts in energy acquisition and allocation can directly impact individuals' reproductive abilities and survival (Magnhagen, 1991; Preisser et al., 2005). Trade-offs between reproductive investment and predation risk and between starvation and predation risk are thus central to many decisions individual prey make regarding habitat choice, foraging and mating (Krams et al., 2013), ultimately leading to

predation risk being key to our understanding of how predators shape the life histories of prey.

Prey selection focuses on the relationship between predators and prey from the predator's perspective. Because each prey item has particular associated hunting costs and energetic benefits to the predator (Werner and Hall, 1974), prey selection can occur at different levels (e.g. predators selecting for different species, size, age or sex classes; predators selecting physically sub-standard individuals) and be influenced by various factors such as the presence of competitors, the habitat structure or the season (see e.g. Creel and Creel, 2002; Fitzgibbon and Fanshawe, 1989; Kruger et al., 1999; Mills and Gorman, 1997; Pole et al., 2004; Radloff and du Toit, 2004). Ultimately, prey selection drives hunting success and the ability of predators to acquire and maintain body reserves, making it a key determinant of predators' individual fitness.

The combination of the numerical response and functional response represents the primary framework for studying how predator and prey populations influence the dynamics of each other, being, to some extent, one of the mathematical outcomes of our understanding of predation risk and prey selection. More precisely, the numerical response aims to capture the effect of prey on predator populations, formulating the increase of predator density with prey density. Functional responses, on the other hand, serve to capture the effect of predators on prey populations, designed to formalize the relationship between prey density and the number of prey eaten by a predator (Holling, 1959a,b). Three types of possible functional responses are generally recognized: (1) Type I assumes predators consume a constant proportion of prey, leading to a linear relationship between the number of prey consumed and prey density; (2) Type II is characterized by a decelerating intake rate of prey consumed as prey density increases, up to a maximum beyond which the number of prey consumed reaches a plateau (i.e. the proportion of prey consumed is assumed to decline with increasing prey density) and (3) Type III is similar to Type II in that saturation occurs at high levels of prey density, but differs from Type II in the sense that at low prey density, predator response to prey is depressed (i.e. the proportion of prey consumed is assumed to increase up to a maximum and then decrease with increasing prey density; see Fig. 1 and Appendix for more information on Holling's functional responses).

Functional and numerical responses are currently integral to our ability to predict predator and prey population dynamics, being also fundamental to our quest to bridge current knowledge gaps found at the interface between



**Figure 1** Holling's functional response curves, labelled with type of response.

population ecology and community ecology. Functional responses are, for example, instrumental in research on the long-term evolution of food webs (Drossel et al., 2004), the existence of facilitation or competition in species assemblages (McCoy et al., 2012; van Langevelde et al., 2008), the persistence of some species at low densities despite heavy predation (Lipcius and Hines, 1986), the potential applicability of biocontrol methods (Putra and Yasuda, 2006; Schenk and Bacher, 2002), the effects of climate change on community stability (Vucic-Pestic et al., 2011), the effects of predator reintroduction on prey populations (Varley and Boyce, 2006) and the mortality rates of predators on game or commercially valuable species (Hayes et al., 2000; Van Ballenberghe and Ballard, 1994). Inaccurate or overly simplified modelling of predator-prey interactions, therefore, can seriously hamper efforts to deepen our understanding of basic community ecology and food web theory, while reducing the adequacy of population dynamics models in supporting wildlife management decisions.

This chapter aims to explore how our current knowledge of the factors shaping prey selection and predation risk relate to current modelling approaches of predator-prey dynamics, focusing in particular on the functional response. We will here concentrate our efforts on identifying the overall importance of the interactions between predation and individual heterogeneity, and discuss their possible role in shaping the dynamics of predator and prey populations. We will consider primarily observational studies of free-ranging vertebrate populations, but, where appropriate, will also draw on work from observational and experimental laboratory studies on invertebrates.



## 2. WHAT SHAPES PREDATION RISK AND PREY SELECTION?

### 2.1 Predation risk

An overwhelming amount of evidence gathered on free-ranging vertebrates now allows us to conclude that individual prey from a given population (1) do not always face the same average lifetime predation risk and (2) do not always face the same predation risk as they age or as they grow. Such a level of individual variability in predation risk has been linked to a myriad of phenotypic, behavioural and environmental variables (see [Table 1](#) for examples). [MacLeod and colleagues \(2006\)](#), for example, reported that predation risk increases with body mass in individual house sparrows *Passer domesticus*. Individuals allocating less time to vigilance (e.g. individuals of a given sex or juveniles of many species) as well as individuals with less defensive abilities (e.g. old individuals or those with poor body condition) have then been found to experience increased predation risk. For example, old elk *Cervus elaphus canadensis* ([Wright et al., 2006](#)) and old female bighorn sheep *Ovis canadensis* ([Festa-Bianchet et al., 2006](#)) have been shown to endure higher predation risk than prime-age adults. Behavioural differences according to the sex of the individual have moreover been found to heighten risk of predation. In the Serengeti National Park, Tanzania, male Thomson's gazelles *Gazella thomsonii* have a greater risk of predation from cheetahs *Acinonyx jubatus*, due to their tendency to be positioned alone on the periphery of groups of gazelles as well as their tendency to be less vigilant than female individuals ([Fitzgibbon, 1990](#)).

Behavioural differences linked to variation in the phenotypic attributes or personalities of individual prey may moreover alter their risk of predation. For example, boldness in bighorn ewes reduces their susceptibility to predation ([Réale and Festa-Bianchet, 2003](#)). Male roe deer *Capreolus capreolus* fawns are more active than females and suffer twice the predation rate from red foxes *Vulpes vulpes* than females ([Aanes and Andersen, 1996](#)). Morphologically similar prey can also vary their behaviour as a response to exposure to predators. Squirrel tree frog tadpoles *Hyla squirella* that had been exposed to chemical cues from their odonate predators had lower activity levels than naïve conspecifics and therefore suffered lower attack rates ([McCoy and Bolker, 2008](#)).

Furthermore, spatiotemporal variation in environmental conditions, habitat type and resource availability may influence predation risk of

**Table 1** Examples of phenotypic and behavioural attributes structuring individual variability in predation risk and prey selection in free-ranging populations

Parameter	Prey species	Individual attribute	Reference
Predation risk	Thomson's gazelle <i>Gazella thomsonii</i>	Sex	Fitzgibbon (1990)
Predation risk	Moose <i>Alces alces</i>	Year of birth	Thompson and Peterson (1988)
Predation risk	White-tailed deer <i>Odocoileus virginianus</i>	Mother's experience	Ozoga and Verme (1986)
Predation risk	Caribou <i>Rangifer tarandus</i>	Birth date	Adams et al. (1995)
Predation risk	Bighorn sheep <i>Ovis canadensis</i>	Age	Réale and Festa-Bianchet (2003)
	Elk <i>Cervus elaphus canadensis</i>		Festa-Bianchet et al. (2006)
			Wright et al. (2006)
Predation risk	Bighorn sheep	Personality	Réale and Festa-Bianchet (2003)
Predation risk	Moose Elk	Habitat	Berger (2007) Hebblewhite et al. (2005)
Predation risk	House sparrow <i>Passer domesticus</i>	Body mass	MacLeod et al. (2006)
Predation risk	Snowshoe hare <i>Lepus americanus</i>	Body condition	Murray (2002)
Predation risk	Feral horse <i>Equus caballus</i>	Coat colour	Turner and Morrison (2001)
Prey selection	Cougar <i>Puma concolor</i>	Age	Ross et al. (1997)
Prey selection	Cheetah <i>Acinonyx jubatus</i>	Sex	Cooper et al. (2007)
Prey selection	Cougar Lynx <i>Lynx lynx</i>	Reproductive status	Pierce et al. (2000) Nilsen et al. (2009)
Prey selection	Blood python <i>Python brongersmai</i>	Colour	Shine et al. (1998)

**Table 1** Examples of phenotypic and behavioural attributes structuring individual variability in predation risk and prey selection in free-ranging populations—cont'd

Parameter	Prey species	Individual attribute	Reference
Prey selection	Oystercatcher <i>Haematopus ostralegus</i>	Dominance/social status	Sutherland et al. (1996) Sautolis et al. (2000)
	Killer whale <i>Orcinus orca</i>		
Prey selection	American robin <i>Turdus migratorius</i>	Body size	Jung (1992)
Prey selection	American pine marten <i>Martes americana</i>	Territory location	Ben-David et al. (1997)

individual prey. Habitat characteristics are indeed of major importance to predator–prey interactions (Gorini et al., 2012). Refuges provide areas where prey can escape from predation pressure, reducing prey availability. Habitat characteristics can also influence detection of prey by predators and their hunting success, altogether influencing predation risk. Grey wolves *Canis lupus* were, for example, more likely to encounter elks in lower elevations than in higher ones in Alberta, Canada, while elks had a different chance of being killed depending on whether they were encountered in grasslands, pine stands or open conifer stands (Hebblewhite et al., 2005). In the winter months in Yellowstone National Park, USA, elk also experienced heightened rates of predation from wolves, due to the comparatively limited mobility of elk compared with wolves in deep snow cover (Wilmers and Getz, 2005). Importantly, individuals can use different habitats depending on their age or size (Englund and Krupa, 2000; Heithaus and Dill, 2002; Montgomery et al., 2013; Sweitzer and Berger, 1992), nutritional need (Barten et al., 2001), life history strategy (Daverat et al., 2006) or reproductive status (Berger, 1991), and such co-variation can underpin a certain amount of individual variability in predation risk. Bighorn ewes with offspring are, for example, less likely to utilize dangerous foraging areas than lone females (Berger, 1991), while predation threat by toadfish *Opsanus tau* on mud crabs *Panopeus herbstii* led smaller crabs to consistently use refuges more than larger ones (Toscano et al., 2014).

## 2.2 Prey selection

Dynamic interactions exist between prey behavioural response to predation and predators' behaviour, resource specialization and distributions, and thus

prey selection by individual predators (Abrams, 2000; Lima, 2002). Decades of research on predator–prey interactions has indeed revealed that individual predators (1) do not all display similar patterns in prey selection and (2) can change patterns in prey selection as they age or as they grow (Pettorelli et al., 2011; see Table 1 for examples). Because natural selection acts on individuals, variance in diet among individuals can have several ecological, evolutionary and management implications through its contribution to differences in individual fitness (Bolnick et al., 2003).

Prey selection is indeed shaped by the trade-off between an individual's energetic requirements and the associated costs of hunting, capturing and consuming prey (MacArthur and Pianka, 1966). The major metabolic life history constraint to prey selection as a result of this fundamental trade-off is a predator's body mass, with increasing mass and locomotive capability resulting in a greater benefit to larger predators from selecting larger prey items (Carbone et al., 1999). Large predatory fishes *Crenicichla alta* have, for example, been reported to prey predominantly on large sexually mature size classes of guppies *Poecilia reticulata* (Reznick et al., 1990), meaning that vulnerability to predation increases with body size in guppies. However, such a relationship between prey body size and prey selection by predators does not always necessitate their specialization on larger prey species. Instead, it has been found that larger predators exploit a wider range of prey species and sizes (Radloff and du Toit, 2004), increasing the potential for both individual specialization and opportunistic offtake in prey selection for larger predators (Sinclair et al., 2003). Differences in prey selection have also been reported according to the sex of predators, some linked to differences emerging from the existence of sexual dimorphism in the predator species considered. In vertebrates, the usually larger-bodied male predators require higher protein diets than females of the same species (Nagy, 1987). This can result in greater prey specialization for female individuals while males can have a propensity to opportunistically take higher-quality (higher protein content) prey; male polar bears *Ursus maritimus* were, for example, found to exhibit much greater dietary variability than females, whose diets were more strongly constrained to ringed seal *Pusa hispida* individuals (Thiemann et al., 2011). Likewise, female Adélie penguins *Pygoscelis adeliae* showed much greater specialization on krill *Euphausia* sp. than males (Clarke et al., 1998). Similarly, a predator's age may influence its prey selection, with younger individuals being smaller in size and having less hunting experience to capture larger prey; for example, juvenile bobcats *Felis rufus* have been found to exhibit greater selection for small- and medium-sized prey than

adult individuals ([Litvaitis et al., 1986](#)). The reproductive status of individual predators can also matter when it comes to prey selection: female cougars *Puma concolor* with offspring preferentially select female deer, while males and females without offspring do not ([Pierce et al., 2000](#)). Individual variability in prey selection has yet sometimes been reported without any obvious correlation with phenotypic attributes: neighbouring kestrels *Falco tinnunculus* were, for example, reported to show consistent differences in prey selection, even though the birds were sharing the same hunting grounds ([Constantini et al., 2005](#)). This may, however, be a result of the individuals' increasing niche exploitation through reducing intraspecific competition; it is proposed that through this process, populations of generalist predators may be in reality clusters of highly specialized individuals (the niche variation hypothesis: [Bolnick et al., 2003, 2007](#)).

Behavioural differences between species, populations and individual predators can then represent an important source of variation in prey selection. The type of prey that it is possible for predators to consume can be influenced by the sociality of the predator in question, with group-living predators more able to capture and kill larger prey. Furthermore, the group size of individual predator groups can influence their prey selection: in the Serengeti National Park, small groups of lions *Panthera leo* seem unable to kill buffalos *Synacerus caffer*, yet the species is an important prey item for larger lion prides ([Packer et al., 1990](#); [Scheel and Packer, 1991](#)). Behavioural differences in individuals' prey selection can moreover be driven by learning. For example, distinct specialization on particular prey types in sea otters *Enhydra lutris* has been found to be passed through matriarchal lineages ([Estes et al., 2003](#)), and hunting techniques and prey selection can vary markedly between killer whale *Orcinus orca* populations ([Sautolis et al., 2000](#)). The presence of competition from other predators of the same species or of other species can also alter individuals' prey selection: for example, [Bolnick and colleagues \(2007\)](#) found that release from inter-specific competition can result in increased dietary generalism.

Environmental factors can also influence prey selection. Indeed, [Andruskiw and colleagues \(2008\)](#) showed that the frequency of prey encounter, prey attack and prey kill by martens *Martes americana* were higher in old uncut forests, despite the fact that red-backed vole *Clethrionomys gapperi* density was similar to that in younger logged forests. Heterogeneous distribution of prey was also reported to result in prey switching and temporary dietary specialism in juvenile silver perch *Bidyanus bidyanus* ([Warburton et al., 1998](#)). Work in Alaska then shows that yearling coho

salmon *Oncorhynchus kisutch* grow faster in warm streams than in nearby cold streams, making them more likely to grow enough in spring and early summer to be able to exploit the glut of eggs from spawning sockeye salmon in August (Armstrong et al., 2010). Coho that do not grow enough are too small to eat eggs and are limited to a diet of insects. Phenotypic attributes coupled with information on environmental conditions can also be key to understanding patterns of prey selection: in Hwange National Park, Zimbabwe, lions are able to kill juvenile elephants *Loxodonta africana* only during very dry periods, and though sometimes they are killed by solitary male lions, in general it is mostly the larger prides that are able to bring them down (Loveridge et al., 2006).

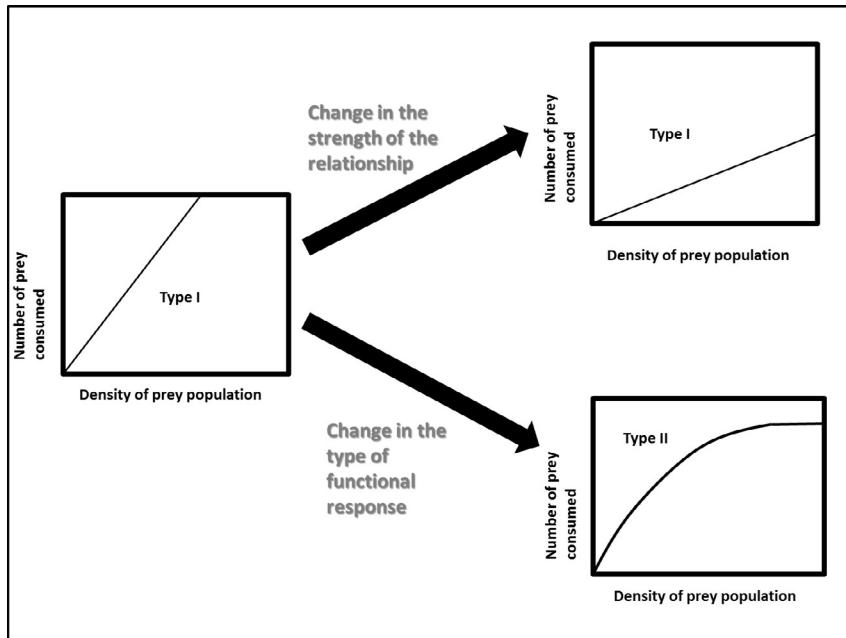


### 3. INDIVIDUAL VARIABILITY AND FUNCTIONAL RESPONSES

In Section 2, we established that individual variability in predation risk and prey selection is common in free-ranging populations, and that such variability tends to be shaped by differences in phenotypic and behavioural attributes, as well as environmental factors. How can such variability be expected to influence functional responses? The importance of individual variability in functional responses was actually recognized early on by Holling (1961), who postulated that characteristics of the prey and predator species, as well as the environment, would affect the functional response. There are two main situations that can be expected to arise: in the first case, individual variability in predation risk and/or prey selection leads to different levels of predation rates among predators and thus differences in the strength of the same functional response. In the second case, individual variability in predation risk and/or prey selection leads to individual predators displaying different types of functional responses (Fig. 2).

#### 3.1 Impact on the strength of the response

Has the existence of groups of predators displaying different strengths of the same functional response been reported in experimental or observational studies so far? The answer is yes. Work on larval ladybeetles *Coccinella septempunctata* (Xia et al., 2003) and *Chaoborus americanus* larvae (Spitze, 1985), for example, shows that larger predators or those hunting larger prey tend to have higher predation rates than smaller conspecifics or those hunting smaller prey. Similarly, an increased number of hunting individuals lowers kill rates of lions (Fryxell et al., 2007) and wolves (Hayes et al., 2000). When



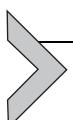
**Figure 2** Possible impacts of individual variability in predation risk and/or prey selection on the functional response. In the first case, individual variability in predation risk and/or prey selection leads to different levels of predation rates among predators and thus differences in the strength of the same functional response (in this case, Type I). In the second case, individual variability in predation risk and/or prey selection leads to individual predators displaying different types of functional responses.

hunting individually, male weasels *Mustela nivalis nivalis* had higher predation rates than females (Sundell, 2003), while female wolf spiders *Pardosa vancouveri* had higher rates than males (Hardman and Turnbull, 1974). Both age and hunger level can then impact predation rates: starved damselflies *Ischnura elegans* had higher predation rates than satiated conspecifics (Akre and Johnson, 1979; see also Bressenford and Toft, 2011); sub-adult pumas have lower kill rates than adults, possibly because experience makes pumas more effective predators (Knopff et al., 2010). As with predation risk and prey selection, predation rate thus seems to vary between individuals and such variability can be structured according to phenotypic attributes.

### 3.2 Impact on the type of response

Few studies have explicitly examined how individuals vary in the type of functional response they exhibit, but there are suggestions that this kind of

variability may not be uncommon, especially among species that exhibit prey switching with size or age. For example, owing to changing nutritional needs during different life stages, adult wolf spiders *Pardosa amentata* have a Type II functional response for protein-rich fruit flies *Drosophila melanogaster* and a dome-shaped response for lipid-rich fruit flies, while sub-adult spiders display the opposite pattern (Bressenford and Toft, 2011). Putra and Yasuda (2006) examined larval hoverflies *Eupeodes corolla* preying on aphids *Acyrthosiphon pisum* and found that first instars had a unimodal response to prey density, second instars had a Type II curve, and third instars had a Type I (linear) response. Observations so far also suggest that individual heterogeneity may produce shapes of functional response beyond those commonly recognized. Rudolf (2008) studied dragonfly *Anax junius* and damselfly *Enallagma aspersum* larvae and found that when the prey were considered as an homogeneous whole, the functional response for the dragonflies and damselflies was a Type III, but when the prey were split by size classes, the functional response pattern did not fit any of the standard forms. This, however, may be due to violations of model assumptions, as was suggested when the response for sub-adult bald eagles *Haliaeetus leucocephalus* scavenging sockeye salmon *Oncorhynchus nerka* could not be characterized (Restani et al., 2000). Blue crabs *Callinectes sapidus* are also particularly variable in their responses according to prey type, prey spatiotemporal distribution, sex of crab and ambient environmental conditions. Not only do they have a Type II response preying on clams *Mya arenaria* buried in mud and a Type III when they were buried in sand (Lipcius and Hines, 1986), but at low oyster *Crassostrea virginica* density, male blue crabs exhibited a Type II response and females a Type III (Eggleston, 1990a); they then exhibited a Type II at low and high temperatures and Type III at intermediate temperature (Eggleston, 1990b).



#### 4. ACCOUNTING FOR INDIVIDUAL VARIABILITY WHEN MODELLING PREDATOR-PREY INTERACTIONS

Does the existence of individual variation in prey selection, predation risk and functional responses really matter when it comes to modelling predator and prey population dynamics and understanding the impact of predation on evolutionary trajectories of both predators and prey? Studies so far have emphasized that accounting for individual heterogeneity can have important theoretical and practical implications in terms of sharpening our understanding of evolution, and population and community ecology. From a management perspective, inter-individual differences can affect

predator impacts on prey (MacNulty et al., 2009), leading researchers and managers who ignore this type of variability to potentially under- or overestimate the expected impacts of predators on prey populations (Okuyama, 2008). A good example of such a situation is provided by individual cougars specializing on bighorn sheep in Canada (Festa-Bianchet et al., 2006). In this situation, predator control programmes aimed at decreasing cougar densities at large scales are unlikely to reduce predation pressure on bighorn sheep, if the specialized individuals are missed by such programmes; however, such a management action could have drastic consequences on the overall predators' population structure and functioning (Robinson et al., 2008). From a theoretical perspective, Bolnick and colleagues (2011) elegantly showed how manipulating the level of individual variability in predators' attack rate or handling time can actually increase or decrease predation pressure, affecting the severity of predator–prey oscillations. Large population oscillations are frequent in many models of predator–prey systems, yet occur relatively rarely in the wild (but see Arditi and Ginzburg, 2012; Holt, 2011). This may be due to the stabilizing effects of complex individual interactions between predators and prey. Accounting for this individual variability in predator–prey models may thus minimize the disconnect between patterns seen in theoretical/experimental versus wild populations. Individual variability in both predation risk and prey selection could also represent a general mechanism maintaining the diversity of the phenotypic traits associated with this variability (e.g. personality type) within populations, something that is beginning to be explored (Pruett et al., 2012). Importantly, if individual variability strongly structures variability in handling time and attack rate, current model assumptions are likely to be violated (McPhee et al., 2011). For example, if both attack rate and handling time are highly variable from one individual predator to the next, then population average predation rates are unlikely to be helpful in making mechanistic interpretations about predator–prey interactions, because multiple combinations of attack rate and handling time will result in the same functional response curve (Okuyama, 2012; see also Table A.2 in the Appendix). Violations of assumptions are, however, rarely examined, and functional response models are often used regardless of whether the assumed behavioural mechanisms behind them are actually operating or not (Okuyama, 2009). This can lead to inaccurate or implausible parameter estimates, thus making it impossible to scale up predictions from the individual to the community level (Okuyama, 2008, 2012).

Despite the recognition that accounting for individual variability in predator–prey interactions may be important, only a quick review of the

literature demonstrates that most population dynamics models aimed at predicting dynamics of prey in the presence of predators consider predators as being identical individuals. Individual variability in predator choice, for example, is generally overlooked, and conservation strategies are traditionally based on identifying average resource requirements for a population (Bolnick et al., 2003; Durell, 2000). Both individual variability within predators and within prey are classically ignored (see e.g. Fryxell et al., 2007; Nilsen et al., 2005; Post et al., 1999; Stenseth et al., 1997; Vucetich et al., 2005, 2011; but see Chesson, 1978 for an exception); instead a population mean is generally used for parameter values (Messier, 1994). Some models do account for certain types of variability such as age class or sex (see e.g. Nilsen et al., 2007; Post et al., 1999), but models accounting for individual variability within predefined groups are extremely rare, even though such levels of variability can be demonstrably large (Akre and Johnson, 1979; Eggleston, 1990a; Restani et al., 2000).

Do modelling frameworks that enable us to take into account such a level of complexity in predator–prey interactions exist? As discussed above, models have been developed that take into account individual variability in susceptibility to predation: these approaches are generally based on (1) attributing different predation susceptibility to only a limited number of phenotypic categories, or (2) at each time step, randomly attributing to each individual prey a different probability of being predated (see e.g. Abrams, 2007). By randomly attributing probabilities at each time step, the second approach might dismiss potential temporal autocorrelation in each individual’s ability to escape predators, but such an approach might be well adapted if a high degree of individual variability in prey selection is expected. Another possible framework enabling explicit consideration of individual variability in predation risk could be based on defining a relative measure of susceptibility to predation for individual prey analogous to frailty, *sensu* Vaupel and colleagues (1979), and consider it as an age-invariant trait (i.e. each individual in a population has a fixed value of relative susceptibility throughout its lifespan). This approach first requires that the level of individual variability in susceptibility to predation is assessed, by collating information on age-specific mortality causes in predated populations and by identifying individuals that died through predation from individuals that died from other causes, such as disease or accidents. Such data can be difficult to access, however, particularly for free-ranging populations. One possible exception is provided by radio-telemetry or GPS-based studies, assuming that radio-collaring does not influence the vulnerability of prey to predation (see e.g. Table 2).

**Table 2** Examples of radio-telemetry or GPS-based studies that quantify the relative importance of predation (indexed as the % of deaths due to predation) as the cause of mortality

Species	Parameter	N	Nd	% of deaths due to predation	Reference
Moose <i>Alces alces</i>	Calf mortality	62	39	92	Bertram and Vivion (2002)
Moose	Adult female mortality	30	7	86	Bertram and Vivion (2002)
Pronghorn <i>Antilocapra americana</i>	Calf mortality	104	87	86	Gregg et al. (2001)
Mule deer <i>Odocoileus hemionus</i>	Adult mortality	43	21	62	Robinson et al. (2002)
White-tailed deer <i>Odocoileus virginianus</i>	Adult mortality	27	13	46	Robinson et al. (2002)
White-tailed deer	≥0.6-year-old female mortality	153	97	48	DelGuidice et al. (2002)
White-tailed deer	Fawn mortality	29	14	59	Long et al. (1998)
White-tailed deer	Adult mortality	112	46	37	Patterson et al. (2002)
Elk <i>Cervus elaphus canadensis</i>	Calf mortality	127	65	45	Singer et al. (1997)
Roe deer <i>Capreolus capreolus</i>	Fawn mortality	151	45	73	Panzacchi et al. (2008)
Caribou <i>Rangifer tarandus</i>	Calf mortality	46	15	55	Mahoney and Virgl (2003)
Reindeer	Calf mortality	621	43	53	Norberg et al. (2006)
Snowshoe hare <i>Lepus americanus</i>	Mortality	177	115	97	Griffin et al. (2005)

In this table, N represents the number of individuals fitted with radio-collars while Nd represents the number of individuals fitted with radio-collars that died.

Recent developments of multi-event capture–recapture models (Pradel, 2005) might also provide a basis for estimating the relative susceptibility of individuals to predation when detection probability is less than 1. Within a defined class (e.g. sex, cohort), the probability of being predated could be

modelled as a function of age or size (which are commonly reported to influence absolute susceptibility to predation). Since each individual only contributes to one data point in the data set, the distribution of the residuals (between the observed and predicted probabilities of being predated) provides the distribution of the individual susceptibilities to predation. [Vaupel and colleagues \(1979\)](#) originally assumed these susceptibilities to be gamma distributed. Considering various values for  $k$  ( $k$  and  $\lambda$  being the parameters of the gamma distribution, with  $k$  measuring the degree of individual heterogeneity in susceptibility to predation), it is then possible to compare (1) the distribution of the observed mortality rates according to age within a category and (2) the expected distribution of mortality rates according to age, with the best fit then enabling the parameterization of the degree of individual heterogeneity in susceptibility to predation within an age-invariant phenotypic category.

Incorporating a large number of variables (e.g. size, sex and habitat use) into the functional response itself remains, however, mostly unexplored territory. Several modelling techniques, such as structural equation modelling ([Grace et al., 2010](#)), Individual-Based Models (IBMs; [Grimm & Railsback, 2013](#)) and linear mixed models, have not been used traditionally in functional response modelling and may hold the potential to begin to address this problem. For situations when there are data on individual animals or groups of animals, mixed-effects models may indeed be used to determine how much of the variance in a parameter, such as attack rate or handling time, is due to differences among individuals. Mixed-effects models can also be used to estimate the importance of factors such as size, sex or habitat use on attack rate or handling time, while controlling for unexplained differences between individuals. IBMs have been used to examine how differences in morphology and behaviour among individuals can impact predator–prey interactions and population dynamics ([DeAngelis and Mooij, 2005; McCauley et al., 1993](#)). While there has been limited use of IBMs in functional response research, [Petersen and De Angelis \(1992\)](#) used them to investigate squawfish *Ptychocheilus oregonensis* predation on juvenile salmon in the Columbia River. They incorporated individual differences in predator feeding rate and timing, and predator and prey size to attempt to distinguish between Type II and III responses. IBMs can be used for theoretical and practical explorations of how behaviours that differ among individual predators affect their encounter and attack rates, handling time and predation rate, and, implemented with care, could provide mechanistic insight into the impact of heterogeneity across individuals on

population processes. With the addition of parameter estimates from field or experimental data, they have potential to make predictions about how demographic or environmental changes could impact functional response and dynamics of specific populations.



## 5. CONCLUSIONS

Our message is simple: predator–prey interactions are complex, much more complex than previously thought. Future research efforts should be focused on exploring how this complexity can best be incorporated into rigorous modelling approaches to improve our ability to predict fluctuations in predators and prey numbers. Predation data from current long-term studies that keep track of individuals in the wild, coupled with innovative modelling techniques, are of paramount importance to improving our understanding of the impacts of individual heterogeneity on population responses (Table 3). Most research so far has focused on the differences between individuals of one species of predator and prey. However, a deeper understanding of predator–prey interactions will require careful study of how the differences in morphological traits and/or behavioural plasticity of both individual predators and prey affect their relationships (see McGhee et al., 2013 for an example). Scaling up from the population level to communities, where empirical data on the functional responses of multiple interacting species are rare, will however likely remain a major challenge for some time. Yet the variation seen in predator–prey interactions suggests that each predator–prey relationship can contribute in unexpected ways to increasing the complexity of biological systems, potentially leading to outcomes we currently fail to predict.

Interestingly, the re-establishment of large predators in many ecosystems (e.g. Breitenmoser, 1998; Valière et al., 2003) and the observed increase in population size of a range of predator species following large-scale cessation of predator control (e.g. Wright, 1999) may provide ecologists and wildlife managers with some fantastic opportunities to tackle the current lack of information regarding the importance of predation in shaping life history traits of free-ranging vertebrates (Pettorelli et al., 2011); to test theories developed using experimental settings and simulation work; to examine how individual variability in both predators and prey impact the interactions between them and to develop tools and frameworks allowing for better integration of the complexity of predator–prey interactions in applied situations (see e.g. MacLeod et al., 2014). Of particular interest is the exploration of the

**Table 3** Non-exhaustive list of key research questions that still require adequate collection of relevant data in the wild in order to be addressed

Questions	Potential issues
Does the presence of predators lead to differences in the means and variation in survival and recruitment rates among phenotypic categories within a prey population? Does it affect the trade-off between survival and reproduction?	Potential changes to the effects of density dependence on prey populations that the presence of predators may generate should be accounted for
Are there predator species characteristics that influence the level of individual variability in predator diet?	Meta-analyses based on information on the level of individual variability in predators' populations should account for differences in levels of inter-specific competition
How does the level of individual variability in prey selection correlate with the distribution of indirect costs of predation in the prey population and the heritability of anti-predator-induced traits?	Most long-term projects on large vertebrate populations have been carried out in predator-free environments, reducing opportunities to empirically address this question
What is the relative importance of indirect and direct costs of predation in determining prey population dynamics?	The answer might be a function of predator and prey densities
Do changes in the average composition of the predator population lead to differences in the means and variation in survival and recruitment rates among phenotypic categories within a prey population?	This question is likely to be best answered within a single prey-single predator system where all the required information is accessible over a sufficient time frame
How does individual vulnerability to predation correlate with individual predation costs and prey selection?	Prey selection might not reflect prey preference, leading to potential inter-population differences in the relationships between predation susceptibility and predation costs within populations of selected and preferred prey
Is susceptibility to predation mainly determined by phenotypic attributes, should it be considered as an individual age-invariant characteristic, or is it mainly randomly variable over time for each individual without temporal autocorrelation?	Predator characteristics might influence how susceptibility to predation is structured within prey populations

**Table 3** Non-exhaustive list of key research questions that still require adequate collection of relevant data in the wild in order to be addressed—cont'd

Questions	Potential issues
How do individual differences in both predators and prey impact their interactions? On what temporal/spatial scales are those differences important and what are the implications for community dynamics?	Difficult to get detailed information on both predator and prey in natural systems; species characteristics and level of habitat heterogeneity might be important when tackling this issue

Here, the direct costs of predation refer to the changes in prey mortality due to predation. The indirect costs of predation, on the other hand, refer to the costs of anti-predator behavioural responses of prey, which can be manifest by reduced prey survival, growth or reproduction (Creel and Christianson, 2008).

relative role of the phenotype and the ecological context (notably, whether or not predation is present) in determining life history traits. A recent study by Cote and colleagues (2013) illustrates the importance of understanding such interactions to better predict population dynamics of both predator and prey. Examining the link between phenotypic specialization and dispersal inclination in mosquitofish *Gambusia affinis*, the authors show that dispersing mosquitofish are less social than non-dispersing fish when predation risk is null. However, they also demonstrate how personality-dependent dispersal is negated under predation risk, with dispersers displaying similar personality types to residents in such conditions (Cote et al., 2013). Such results support previous calls, as well as that made here, for more research into assessing and taking into account the potentially individually variable indirect impacts of predation when modelling predator–prey interactions (Creel and Christianson, 2008; Pettorelli et al., 2011).



## APPENDIX

**Table A.1** Holling's three functional responses

Model	Formula	Description
Type I	Kill rate = attack rate*prey density	Linear
Type II	Kill rate = $\frac{\text{attack rate} * \text{prey density}}{1 + \text{attack rate} * \text{prey density} * \text{handling time}}$	Asymptotic
Type III	Kill rate = $\frac{b * \text{prey density}^2}{1 + c * \text{prey density} + b * \text{handling time} * \text{prey density}^2}$	Sigmoid

Note that in these equations,  $b$  and  $c$  are constants.

**Table A.2** Definitions of the parameters used in the functional response equations

Parameter	Definition
Encounter rate	Search rate (area searched/unit time) * prey density (individuals/area)
Attack rate	Encounter rate * proportion of encounters that turn into attacks * proportion of attacks that are successful
Handling time	The time required to handle prey so that other prey cannot be concurrently attacked. May include pursuing, subduing, eating, digesting. Constant in Types II and III
Kill/predation rate	Number of prey killed/predator (individual or group)/unit time. Y axis of functional response curves

## REFERENCES

- Aanes, R., Andersen, R., 1996. The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. *Can. J. Zool.* 74, 1857–1865.
- Abrams, P.A., 2000. The evolution of predator-prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst.* 31, 79–105.
- Abrams, P.A., 2007. Habitat choice in predator-prey systems: spatial instability due to interacting adaptive movements. *Am. Nat.* 169, 581–594.
- Adams, L.G., Singer, F.J., Dale, B.W., 1995. Caribou calf mortality in Denali National Park, Alaska. *J. Wildl. Manage.* 59, 584–594.
- Akre, B.G., Johnson, D.M., 1979. Switching and sigmoid functional response curves by damselfly naiads with alternative prey available. *J. Anim. Ecol.* 48, 703–720.
- Andruskiw, M., Fryxell, J.M., Thompson, I.D., Baker, J.A., 2008. Habitat-mediated variation in predation risk by the American marten. *Ecology* 89, 2273–2280.
- Arditi, R., Ginzburg, L.R., 2012. How Species Interact: Altering the Standard View of Trophic Ecology. Oxford University Press, New York.
- Armstrong, J.B., Schindler, D.E., Omori, K.L., Ruff, C.P., Quinn, T.P., 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology* 91, 1445–1454.
- Barten, N.L., Bowyer, R.T., Jenkins, K.J., 2001. Habitat use by female caribou: trade-offs associated with parturition. *J. Wildl. Manage.* 65, 77–92.
- Ben-David, M., Flynn, R.W., Schell, D.M., 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111, 280–291.
- Berger, J., 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Anim. Behav.* 41, 61–64.
- Berger, J., 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.* 3, 620–623.
- Bertram, M.R., Vivion, M.T., 2002. Moose mortality in eastern interior Alaska. *J. Wildl. Manage.* 66, 747–756.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., Forister, M.L., 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* 161, 1–28.

- Bolnick, D.I., Svänbäck, M., Araujo, J., Persson, J., 2007. More generalized populations are also more heterogeneous: comparative support for the niche variation hypothesis. *Proc. Natl. Acad. Sci. U.S.A.* 104, 10075–10079.
- Bolnick, D.I., Amarasekare, P., Araujo, M.S., Buerger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26, 183–192.
- Breitenmoser, U., 1998. Large predators in the Alps: the fall and rise of man's competitors. *Biol. Conserv.* 3, 279–289.
- Bressenford, B.B., Toft, S., 2011. Dome-shaped functional response induced by nutrient balance of the prey. *Biol. Lett.* 23, 517–520.
- Carbone, C., Mace, G.M., Roberts, S.C., MacDonald, D.W., 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* 402, 286–288.
- Chesson, P.L., 1978. Predator-prey theory and variability. *Annu. Rev. Ecol. Syst.* 9, 323–347.
- Clarke, J., Manly, B., Kerry, K., Gardner, H., Franchi, E., Corsolini, S., Focardi, S., 1998. Sex differences in Adélie penguin foraging strategies. *Polar Biol.* 20, 248–258.
- Constantini, D., Casagrande, S., Di Lieto, G., Fanfani, A., Dell'Osso, G., 2005. Consistent differences in feeding habits between neighbouring breeding kestrels. *Behaviour* 142, 1409–1421.
- Cooper, A.B., Pettorelli, N., Durant, S.M., 2007. Large carnivore menus: factors affecting hunting decisions by cheetahs in the Serengeti. *Anim. Behav.* 73, 651–659.
- Cote, J., Fogarty, S., Tymen, B., Sih, A., Brodin, T., 2013. Personality-dependent dispersal cancelled under predation risk. *Proc. R. Soc. B* 280, 20132349.
- Creel, S., Christianson, D., 2008. Relationships between direct predation and risk effects. *Trends Ecol. Evol.* 23, 194–201.
- Creel, S., Creel, N.M., 2002. *The African Wild Dog: Behaviour, Ecology and Conservation*. Princeton University Press, Princeton.
- Daverat, F., Limburg, K.E., Thibault, I., Shiao, J.-C., Dodson, J.J., Caron, F., Tzeng, W.-N., Iizuka, Y., Wickstrom, H., 2006. Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*. *Mar. Ecol. Prog. Ser.* 308, 231–241.
- DeAngelis, D.L., Mooij, W.M., 2005. Individual-based modeling of ecological and evolutionary processes. *Annu. Rev. Ecol. Evol. Syst.* 36, 147–168.
- DelGuidice, G.D., Riggs, M.R., Jolly, P., Pan, W., 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in North-central Minnesota. *J. Wildl. Manage.* 66, 698–717.
- Drossel, B., McKane, A.J., Quince, C., 2004. The impact of nonlinear functional responses on the long-term evolution of food web structure. *J. Theor. Biol.* 229, 539–548.
- Durell, S.E.A., 2000. Individual feeding specialization in shorebirds: population consequences and conservation implications. *Biol. Rev. Camb. Philos. Soc.* 75, 503–518.
- Egginton, D.B., 1990a. Functional responses of blue crabs *Callinectes sapidus* Rathbun feeding on juvenile oysters *Crassostrea* (Gmelin): effects of predator sex and size, and prey size. *J. Exp. Mar. Biol. Ecol.* 143, 73–90.
- Egginton, D.B., 1990b. Behavioural mechanisms underlying variable functional responses of blue crabs, *Callinectes sapidus* feeding on juvenile oysters, *Crassostrea virginica*. *J. Anim. Ecol.* 59, 615–630.
- Englund, G., Krupa, J.J., 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. *Freshw. Biol.* 43, 75–83.
- Estes, J.A., Riedman, M.L., Staefler, M.M., Tinker, M.T., Lyon, B.E., 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. *J. Anim. Ecol.* 72, 144–155.

- Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J.T., Pelletier, F., 2006. Stochastic predation events and population persistence in bighorn sheep. *Proc. R. Soc. B* 273, 1537–1543.
- Fitzgibbon, C.D., 1990. Why do hunting cheetahs prefer male gazelles? *Anim. Behav.* 40, 837–845.
- Fitzgibbon, C.D., Fanshawe, J.H., 1989. The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. *J. Zool. Soc. Lond.* 218, 99–107.
- Fryxell, J.M., Mosser, A., Sinclair, A.R.E., Packer, C., 2007. Group formation stabilizes predator-prey dynamics. *Nature* 449, 1041–1043.
- William, J.F., Fraser, D.F., 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68, 1856–1862.
- Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M., Nilsen, E.B., 2012. Habitat heterogeneity and mammalian predator-prey interactions. *Mammal Rev.* 42, 55–77.
- Grace, J.B., Anderson, T.M., Olf, H., Scheiner, S.M., 2010. On the specification of structural equation models for ecological systems. *Ecol. Monogr.* 80, 67–87.
- Gregg, M.A., Bray, M., Kilbride, K.M., Dunbar, M.R., 2001. Birth synchrony and survival of pronghorn fawns. *J. Wildl. Manage.* 65, 19–24.
- Griffin, P.C., Griffin, S.C., Waroquiers, C., Mills, L.S., 2005. Mortality by moonlight: predation risk and the snowshoe hare. *Behav. Ecol.* 16, 938–944.
- Grimm, V., Railsback, S.F., 2013. Individual-Based Modeling and Ecology. Princeton University Press, Princeton, 448 pp.
- Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. *Am. Nat.* 94, 421–425.
- Hardman, J.M., Turnbull, A.L., 1974. The interaction of spatial heterogeneity, predator competition and the functional response to prey density in a laboratory system of wolf spiders (Araneae: Lycosidae) and fruit flies (Diptera: Drosophilidae). *J. Anim. Ecol.* 43, 155–171.
- Hayes, R.D., Baer, A.M., Wotschikowsky, U., Harestad, A.S., 2000. Kill rate by wolves on moose in the Yukon. *Can. J. Zool.* 78, 49–59.
- Hebblewhite, M., Merrill, E.H., McDonald, T.L., 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf/elk predator/prey system. *Oikos* 111, 101–111.
- Heithaus, M.R., Dill, L.M., 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83, 480–491.
- Holling, C.S., 1959a. The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. *Can. Entomol.* 91, 293–320.
- Holling, C.S., 1959b. Some characteristic of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398.
- Holling, C.S., 1961. Principles of insect predation. *Annu. Rev. Entomol.* 6, 163–182.
- Holt, R.D., 2011. Natural enemy-victim interactions: do we have a unified theory yet? In: Scheiner, S.M., Willig, M.R. (Eds.), *The Theory of Ecology*. The University of Chicago Press, Chicago, pp. 125–161.
- Jung, R.E., 1992. Individual variation in fruit choice by American robins (*Turdus migratorius*). *Auk* 109, 98–111.
- Knopff, K.H., Knopff, A.A., Kortello, A., Boyce, M.S., 2010. Cougar kill rate and prey composition in a multiprey system. *J. Wildl. Manage.* 74, 1435–1447.
- Krams, I., Kivleniece, I., Kuusik, A., Krama, T., Freeberg, T.M., Mand, R., Vrublevska, J., Rantala, M.J., Mand, M., 2013. Predation selects for low resting metabolic rate and consistent individual differences in anti-predator behaviour in a beetle. *Acta Ethol.* 16, 163–172.

- Kruger, S.C., Lawes, M.J., Maddock, A.H., 1999. Diet choice and capture success of wild dog in Hluhluwe-Umfolozi Park, South Africa. *J. Zool. Soc. Lond.* 248, 543–551.
- Lima, S.L., 2002. Putting predators back into behavioural predator–prey interactions. *Trends Ecol. Evol.* 17, 70–75.
- Lipcius, R.N., Hines, A.H., 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67, 1361–1371.
- Litvaitis, J.A., 2000. Investigating food habits of terrestrial vertebrates. In: Boitani, L., Fuller, T.K. (Eds.), *Research Techniques in Animal Ecology: Controversies and Consequences*. Columbia University Press, New York, pp. 165–190.
- Litvaitis, J.A., Clark, A.G., Hunt, J.H., 1986. Prey selection and fat deposits of bobcats *Felis rufus* during autumn and winter in Maine. *J. Mammal.* 67, 389–392.
- Long, R.A., O'Connell, A.F., Harrison, D.J., 1998. Mortality and survival of white-tailed deer fawns on a north Atlantic coastal island. *Wildl. Biol.* 4, 237–247.
- Loveridge, A.J., Hunt, J.E., Murindagomo, F., MacDonald, D.W., 2006. Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *J. Zool.* 270, 523–530.
- MacArthur, R.H., Pianka, E.R., 1966. On the optimal use of a patchy environment. *Am. Nat.* 100, 603–609.
- MacLeod, R., Barnett, P., Clark, J., Cresswell, W., 2006. Mass-dependent predation risk as a mechanism for house sparrow declines? *Biol. Lett.* 2, 43–46.
- MacLeod, C.D., MacLeod, R., Learmonth, J.A., Cresswell, W., Pierce, G.J., 2014. Predicting population-level risk effects of predation from the responses of individuals. *Ecology* 95, 2006–2015.
- MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R., Packer, C., 2009. Predatory senescence in ageing wolves. *Ecol. Lett.* 12, 1347–1356.
- Magnhagen, C., 1991. Predation risk as a cost of reproduction. *Trends Ecol. Evol.* 6, 183–186.
- Mahoney, S.P., Virgl, J.A., 2003. Habitat selection and demography of a non-migratory woodland caribou population in Newfoundland. *Can. J. Zool.* 81, 321–334.
- May, R.M., 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.
- McCauley, E., Wilson, W.G., de Roos, A.M., 1993. Dynamics of age-structured and spatially structured predator-prey interactions: individual-based models and population-level formulations. *Am. Nat.* 142, 412–442.
- McCoy, M.W., Bolker, B.M., 2008. Trait-mediated interactions: influence of prey size, density and experience. *J. Anim. Ecol.* 77, 478–486.
- McCoy, M.W., Stier, A.C., Osenberg, C.W., 2012. Emergent effects of multiple predators on prey survival: the importance of depletion and the functional response. *Ecol. Lett.* 15, 1449–1456.
- McGhee, K.E., Pintor, L.M., Bell, A.M., 2013. Reciprocal behavioral plasticity and behavioral types during predator-prey interactions. *Am. Nat.* 182, 704–717.
- McPhee, H.M., Webb, N.F., Merrill, E.H., 2011. Time-to-kill: measuring attack rates in a heterogenous landscape with multiple prey types. *Oikos* 121, 711–720.
- Messier, F., 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology* 75, 478–488.
- Mills, M.G.L., Gorman, M.L., 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv. Biol.* 11, 1397–1406.
- Montgomery, R.A., Vucetich, J.A., Peterson, R.O., Roloff, G.J., Millenbah, K.F., 2013. The influence of winter severity, predation and senescence on moose habitat use. *J. Anim. Ecol.* 82, 301–309.
- Mousseau, T.A., Endler, J., Sinervo, B., 2000. *Adaptive Genetic Variation in the Wild*. Oxford University Press, New York, 276 pp.

- Murray, D.L., 2002. Differential body condition and vulnerability to predation in snowshoe hares. *J. Anim. Ecol.* 71, 614–625.
- Nagy, K.A., 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* 57, 111–128.
- Nilsen, E.B., Pettersen, T., Gundersen, H., Milner, J.M., Mysterud, A., Solberg, E.J., Andreassen, H.P., Stenseth, N.C., 2005. Moose harvesting strategies in the presence of wolves. *J. Anim. Ecol.* 42, 389–399.
- Nilsen, E.B., Milner-Gulland, E.J., Schofield, L., Mysterud, A., Stenseth, N.C., Coulson, T.N., 2007. Wolf introduction to Scotland: public attitudes and consequences for red deer management. *Proc. R. Soc. Lond. B* 274, 995–1002.
- Nilsen, E.B., Gaillard, J.-M., Andersen, R., Odden, J., Delorme, D., van Laere, G., Linnell, J.D.C., 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *J. Anim. Ecol.* 78, 585–594.
- Norberg, H., Kojola, I., Aikio, P., Nylund, M., 2006. Predation by golden eagle on semi-domesticated reindeer calves in northeastern Finnish Lapland. *Wildl. Biol.* 12, 393–402.
- Okuyama, T., 2008. Individual behavioral variation in predator-prey models. *Ecol. Res.* 23, 665–671.
- Okuyama, T., 2009. Local interactions between predators and prey call into question commonly used functional responses. *Ecol. Model.* 220, 1182–1188.
- Okuyama, T., 2012. Flexible components of functional responses. *J. Anim. Ecol.* 81, 185–189.
- Ozoga, J.J., Verme, L.J., 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. *J. Wildl. Manage.* 50, 480–486.
- Packer, C., Scheel, D., Pusey, A.E., 1990. Why lions form groups: food is not enough. *Am. Nat.* 136, 1–19.
- Panzacchi, M., Linnell, J.D.C., Odden, J., Andersen, R., 2008. When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. *Can. J. Zool.* 86, 116–126.
- Patterson, B.R., MacDonald, B.A., Lock, B.A., Anderson, D.G., Benjamin, L.K., 2002. Proximate factors limiting population growth of white-tailed deer in Nova Scotia. *J. Wildl. Manage.* 66, 511–521.
- Petersen, J.H., De Angelis, D.L., 1992. Functional response and capture timing in an individual-based model: predation by Northern Squawfish (*Ptychocheilus oregonensis*) on juvenile salmonids in the Columbia River. *Can. J. Fish. Aquat. Sci.* 49, 2551–2565.
- Pettorelli, N., Coulson, T., Durant, S.M., Gaillard, J.-M., 2011. Predation, individual variability and population dynamics. *Oecologia* 167, 305–314.
- Pierce, B.M., Bleich, V.C., Bowyer, R.T., 2000. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. *J. Mammal.* 81, 462–472.
- Pole, A., Gordon, I.J., Gorman, M.L., MacAskill, M., 2004. Prey selection by African wild dogs (*Lycaon pictus*) in southern Zimbabwe. *J. Zool. Soc. Lond.* 262, 207–215.
- Post, E., Peterson, R.O., Stenseth, N.C., McLaren, B.E., 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature* 401, 905–907.
- Pradel, R., 2005. Multievent: an extension of multistate capture-recapture models to uncertain states. *Biometrics* 61, 442–447.
- Preisser, E.L., Bolnick, D.I., Benard, M.F., 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86, 501–509.
- Pruitt, J.N., Stachowicz, J.J., Sih, A., 2012. Behavioral types of predator and prey jointly determine prey survival: potential implications for the maintenance of within-species behavioural variation. *Am. Nat.* 179, 217–227.
- Putra, N.S., Yasuda, H., 2006. Effects of prey species and its density on larval performance of two species of hoverfly larvae, *Episyphus balteatus* de Geer and *Eupeodes corollae* Fabricius (Diptera: Syrphidae). *Appl. Entomol. Zool.* 41, 389–397.

- 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. *J. Anim. Ecol.* 73, 410–423.
- Réale, D., Festa-Bianchet, M., 2003. Predator-induced natural selection on temperament in bighorn ewes. *Anim. Behav.* 65, 463–470.
- Relyea, R.A., 2002. The many faces of predation: how induction, selection, and thinning combine to alter prey phenotypes. *Ecology* 83, 1953–1964.
- Restani, M., Harmata, A.R., Madden, E.M., 2000. Numerical and functional responses of migrant bald eagles exploiting a seasonally congregated food source. *Condor* 102, 561–568.
- Reznick, D.A., Bryga, H., Endler, J.A., 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346, 357–359.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343, 1241484.
- Robinson, H.S., Wielgus, R.B., Gwilliam, J.C., 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. *Can. J. Zool.* 80, 556–568.
- Robinson, H.S., Wielgus, R.B., Cooley, H.S., Cooley, S.W., 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecol. Appl.* 18, 1028–1037.
- Ross, P.I., Jalkotzy, M.G., Festa-Bianchet, M., 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. *Can. J. Zool.* 74, 771–775.
- Rudolf, V.H., 2008. Consequences of size structure in the prey for predator-prey dynamics: the composite functional response. *J. Anim. Ecol.* 77, 520–528.
- Sautinis, E., Matkin, C., Barrett-Lennard, L., Heise, K., Ellis, G., 2000. Foraging strategies of sympatric killer whale populations in Prince William Sound, Alaska. *Mar. Mamm. Sci.* 16, 94–109.
- Scheel, D., Packer, C., 1991. Group hunting behaviour of lions: a search for cooperation. *Anim. Behav.* 41, 697–709.
- Schenk, D., Bacher, S., 2002. Functional response of a generalist insect predator to one of its prey species in the field. *J. Anim. Ecol.* 71, 524–531.
- Schmitz, O.J., 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.* 151, 327–342.
- Shine, R., Ambariyanto, Harlow, P.S., Mumpuni, 1998. Ecological divergence among sympatric colour morphs in blood pythons *Python brongersmai*. *Oecologia* 116, 113–119.
- Sinclair, A.R.E., Mduma, S.A.R., Brashares, J.S., 2003. Patterns of predation in a diverse predator-prey system. *Nature* 425, 288–290.
- Singer, F.J., Harting, A., Symonds, K.K., Coughenour, M.B., 1997. Density-dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *J. Wildl. Manage.* 61, 12–25.
- Spitze, K., 1985. Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. *Ecology* 66, 938–949.
- Stenseth, N.C., Falck, W., Bjørnstad, O.N., Krebs, C.J., 1997. Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx. *Proc. Natl. Acad. Sci. U.S.A.* 94, 5147–5152.
- Sundell, J., 2003. Population dynamics of microtine rodents: an experimental test of the predation hypothesis. *Oikos* 101, 416–427.
- Sutherland, W.J., Ens, B.J., Goss-Custard, J.D., Hulscher, J.B., 1996. Specialization. In: Goss-Custard, J.D. (Ed.), *The Oystercatcher*. Oxford University Press, New York, pp. 105–132.
- Sweitzer, R.A., Berger, J., 1992. Size-related effects of predation on habitat use and behaviour of porcupines *Erethizon dorsatum*. *Ecology* 73, 867–875.

- Thiemann, G.W., Iverson, S.J., Stirling, I., Obbard, M.E., 2011. Individual patterns of prey selection and dietary specialisation in an Arctic marine carnivore. *Oikos* 120, 1469–1478.
- Thompson, I.D., Peterson, R., 1988. Does wolf predation alone limit the moose population in Pukaskwa park? *J. Wildl. Manage.* 52, 556–559.
- Toscano, B.J., Gatto, J., Griffen, B.D., 2014. Effect of predation threat on repeatability of individual crab behaviour revealed by mark-recapture. *Behav. Ecol. Sociobiol.* 68, 519–527.
- Turner Jr., J.W., Morrison, M.L., 2001. Influence of predation by mountain lions on numbers and survivorship of a feral horse population. *Southwest. Nat.* 46, 183–190.
- Valière, N., Fumagalli, L., Gielly, L., Miquel, C., Lequette, B., Poulle, M.-L., Weber, J.-M., Arlettaz, R., Taberlet, P., 2003. Long-distance wolf recolonization of France and Switzerland inferred from non-invasive genetic sampling over a period of 10 years. *Anim. Conserv.* 6, 83–92.
- Van Ballenberghe, V., Ballard, W.B., 1994. Limitation and regulation of moose populations: the role of predation. *Can. J. Zool.* 72, 2071–2077.
- Van Langevelde, F., Drescher, M., Heitkönig, I.M.A., Prins, H.H.T., 2008. Modelling instantaneous intake rate of herbivores as function of forage quality and mass: effects on facilitative and competitive interactions between differently sized herbivores. *Ecol. Modell.* 213, 273–284.
- Varley, N., Boyce, M.S., 2006. Adaptive management for reintroductions: updating a wolf recovery model for Yellowstone National Park. *Ecol. Modell.* 193, 315–339.
- Vaupel, J.W., Manton, K.G., Stallard, E., 1979. The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* 16, 439–454.
- Vucetich, J.A., Smith, D.W., Stahler, D.R., 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos* 111, 259–270.
- Vucetich, J.A., Hebblewhite, M., Smith, D.W., Peterson, R.O., 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. *J. Anim. Ecol.* 80, 1236–1245.
- Vucic-Pestic, O., Ehnes, R.B., Rall, B.C., Brose, U., 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Glob. Change Biol.* 17, 1301–1310.
- Warburton, K., Retif, S., Hume, D., 1998. Generalists as sequential specialists: diets and prey switching in juvenile silver perch. *Environ. Biol. Fishes* 51, 445–454.
- Werner, E.E., Hall, D.J., 1974. Optimal foraging and the size selection of prey by the bluegill sunfish. *Ecology* 55, 1042–1052.
- Wilmers, C.C., Getz, W.M., 2005. Gray wolves as climate change buffers in Yellowstone. *PLoS Biol.* 3, e92.
- Wittmer, H.U., Sinclair, A.R.E., McLellan, B.N., 2005. The role of predation in the decline and extirpation of woodland caribou populations. *Oecologia* 144, 257–267.
- Wright, R.G., 1999. Wildlife management in the national parks: questions in search of answers. *Ecol. Appl.* 9, 30–36.
- Wright, G.J., Peterson, R.O., Smith, D.W., Lemke, T.O., 2006. Selection of northern Yellowstone elk by gray wolves and hunters. *J. Wildl. Manage.* 70, 1070–1078.
- Xia, J.Y., Rabbinge, R., Van Der Werf, W., 2003. Multistage functional responses in a ladybeetle-aphid system: scaling up from the laboratory to the field. *Environ. Entomol.* 32, 151–162.
- Yeakel, J.D., Pires, M.M., Rudolf, L., Dominy, N.J., Kock, P.L., Guimarães Jr., P.R., Gross, T., 2014. Collapse of an ecological network in Ancient Egypt. *Proc. Nat. Acad. Sci. U.S.A.* 111 (40), 14472–14477.