

Predation, individual variability and vertebrate population dynamics

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Abstract Both predation and individual variation in life history traits influence population dynamics. Recent results from laboratory predator–prey systems suggest that differences between individuals can also influence predator–prey dynamics when different genotypes experience different predation-associated mortalities. Despite the growing number of studies in this field, there is no synthesis identifying the overall importance of the interactions between predation and individual heterogeneity and their role in shaping the dynamics of free-ranging populations of vertebrates. We aim to fill this gap with a review that examines how individual variability in prey susceptibility, in predation costs, in predator selectivity, and in predatory performance, might influence prey population dynamics. Based on this review, it is clear that (1) predation risk and

costs experienced by free-ranging prey are associated with their phenotypic attributes, (2) many generalist predator populations consist of individual specialists with part of the specialization associated with their phenotypes, and (3) a complete understanding of the population dynamic consequences of predation may require information on individual variability in prey selection and prey vulnerability. Altogether, this work (1) highlights the importance of maintaining long-term, detailed studies of individuals of both predators and prey in contrasting ecological conditions, and (2) advocates for a better use of available information to account for interactive effects between predators and their prey when modelling prey population dynamics.

Keywords Predator–prey interactions · Wildlife management · Demography · Phenotype · Trophic cascades

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Introduction

Population and evolutionary dynamics influence each other when phenotypic traits are associated with components of fitness. A growing number of studies have begun to quantify the contribution of genetic or phenotypic variation to population growth (Coulson et al. 2006; Pelletier et al. 2007) and dynamics (Hairston et al. 2005; Hanski and Saccheri 2006). Such studies have applied consequences, providing results that can help with managing wildlife and predicting changes in biodiversity in the face of environmental change. There is consequently substantial interest in characterizing the factors influencing variation in population size.

The re-establishment of large predators in many ecosystems (e.g. Breitenmoser 1998; Valière et al. 2003) and

the observed increase in the population sizes of a range of predator species following the large-scale cessation of predator control (e.g. Wright 1999) have revived the interest of mammalian population ecologists and wildlife managers in the dynamics of predation (e.g. Vucetich et al. 2005; Nilsen et al. 2007, 2009; MacNulty et al. 2009). Predation plays a key role in shaping animal populations and communities through predator arrival timing, prey killed, and through the behavioural and life history decisions of both predators and prey (Lima and Dill 1990; Fryxell and Lundberg 1994; Olito and Fukami 2009). Predators can affect prey demography both through predation-associated mortality (direct effects; Krivan and Eisner 2003) and through the costs of anti-predator behavioural and physiological responses (indirect effects; Creel and Christianson 2008). The direct effects of predation on prey population dynamics can be dramatic (Sinclair et al. 2003; Wittmer et al. 2005); in contrast, the indirect effects of predation on prey population dynamics are generally less obvious. Previous studies on mammals have suggested that indirect effects might influence population dynamics through changes in habitat use (Creel et al. 2005; Fortin et al. 2005), but the empirical evidence for a quantitative impact on vertebrates' population growth rate is still limited (Creel et al. 2007; Creel and Christianson 2008; but see Preisser et al. 2005 and Fievet et al. 2008 for empirical evidence of indirect effects of predation). Predation can also 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 (Reznick et al. 1990; Relyea 2002). The classical island rule model, which accounts for opposite trends in the body size evolution of small and large mammalian prey on islands for example, invokes differences in predation pressure (Raia and Meiri 2006).

When it comes to the consideration of predation as a factor shaping free-ranging vertebrate population dynamics, most models consider predators to be identical individuals (having the same relative impact on prey; Post et al. 1999; Nilsen et al. 2005; Vucetich et al. 2005; Fryxell et al. 2007), and individual variability in predator choice is generally overlooked, reflecting maybe a wider neglect of the ecological significance of dietary specializations within wildlife populations (Bolnick et al. 2003). The effect of prey on predator populations is generally modelled using numerical responses (Holling 1959), which describe changes in predator numbers or densities with changes in prey numbers or densities (Messier 1994). On the other hand, the direct effect of predators on prey populations (i.e. number of prey killed) is generally modelled as a function of the per capita kill rate and predator density, and this per capita kill rate (i.e. predator

killing efficiency) is modelled using functional responses (Holling 1959). Functional responses thus describe changes in feeding behaviour of individual predators with changes in prey availability (Messier 1994). Individual prey are either considered to be identical individuals (e.g. Stenseth et al. 1997; Kelly and Durant 2000) or individuals that display different probabilities of being predated (mostly according to age or sex; e.g. Post et al. 1999; Nilsen et al. 2007).

Such simplicity does not echo the myriad of studies highlighting the importance of individual variability in understanding population size variation (Lomnicki 1988; Gaillard et al. 2000; Cam et al. 2002; Nussey et al. 2008) or predator's diet (Bolnick et al. 2003, 2007), and it is relatively surprising to note that while both predation and individual differences have been demonstrated to impact population dynamics, their interactions have rarely been considered, despite substantial potential for these two processes to combine to influence prey population dynamics. Recent results from laboratory predator–prey systems do indeed suggest that differences between individuals can influence predator–prey dynamics, with different genotypes experiencing different predation-associated mortalities (Reznick et al. 1990; Bonsall 2003; Yoshida et al. 2003; Fussmann et al. 2005). To fill this gap, we (1) review how individual variability might affect predator–prey interactions, and (2) present a qualitative perspective of opportunities and needs for (a) a better understanding of predator–prey dynamics in the wild and (b) a better integration of individual-based information while developing predator–prey population models. We do so considering primarily observational studies of free-ranging vertebrate populations, but, where appropriate, also draw on work from experimental laboratory studies on invertebrates.

Prey vulnerability and individual differences

Back to the theory: predation risk, costs of predation and trait induction

Organisms are expected to follow several rules: they generally try to maximize their energy intake per unit time, while minimizing the energetic costs linked to foraging activity and their probability of being predated. These rules apply to both predators and prey, are expressed on the individual scale, and shape predation risk for prey. First, the trade-off between gaining energy and avoiding predation is central to the concept of predation risk and is expected to influence survivorship of prey (Houston et al. 1993), as foraging can be a “risky” activity (lower vigilance, potential co-variation between habitat

quality and predator density; Fraser and Huntingford 1986). Second, each prey item has particular associated hunting costs and energetic benefits to the predator (Werner and Hall 1974), and bigger prey involving relatively low hunting costs for high energy incomes are expected to be selected by predators. These two simple rules lead to predation risk being shaped by a range of interrelated components (Lima and Dill 1990; Houston et al. 1993; Luttbeg and Schmitz 2000; Husseman et al. 2003; Sih et al. 2004a, b), including individual prey phenotype (e.g. sex, age, size), prey behaviour, individual predator phenotype (e.g. gape size, hunting tactic), predator behaviour, and the local conditions experienced by both predator and prey (e.g. prey group size, availability of cover for ambush hunting).

Predation risk is key to understanding prey population dynamics, but not just through prey killed by predators. Predation risk also constrains animals and compromises the ability of prey to acquire and maintain body reserves by hindering foraging efficiency and increasing physiological stress, generating energetic and physiological consequences (generally referred to as indirect costs of predation; Creel and Christianson 2008). Anti-predator tactics can modify habitat selection (Gilliam and Fraser 1987) and change trophic flows by altering diet selection (Schmitz 1998), and indirect costs of predation can include reduced energy intake, higher energetic allocation to predator avoidance, and lower mating and reproductive success (Magnhagen 1991; Preisser et al. 2005).

Demographic differences between individuals drive evolution, and by influencing trait distribution and population growth rates, predators play an active role in shaping their prey. Predators do indeed affect the evolution of behaviour, life history, physiology, and morphology of their prey (Magurran 1999); predators can directly induce prey phenotypes through visual and chemical cues, they can indirectly alter prey phenotypes by thinning the prey population (thereby reducing competition), and they can cause selection on prey phenotypes through non-random killing (Relyea 2002). Nonlethal effects of predators resulting in trait modifications in prey are referred to as “trait-mediated” effects, and such effects can modify the interaction between predators and prey, leading sometimes to dramatic changes in population sizes for both prey and predators (Abrams 1995; Peacor 2002). Predator phenotypes can shape prey evolution, and predation can for instance induce opposite changes in prey growth patterns according to gape size constraints experienced by the predator (Urban 2007). Induced anti-predator phenotypes can be associated with substantial costs for prey, but evidence suggests that certain types of induced traits (behavioural, morphological) might be reversible (Relyea 2003).

Individual variability in the wild: not all prey are equal

Individual variability in predation risk

Theoretical and experimental research have highlighted the fact that a lot of variables have the potential to shape predation risk, suggesting that individual prey cannot be considered equal in terms of vulnerability to predation. Such inequality might be related to the fact that individuals do not face the same “average” lifetime predation risk (due for example to differences among sexes, personality types, or habitat), and/or to the fact that they do not face the same predation risk as they age. But has this variability been reported in free-ranging vertebrates? The answer is yes, with evidence of both processes occurring. Adult male Thomson’s gazelles *Gazella thomsonii* systematically experience higher predation risk than females, because cheetahs *Acinonyx jubatus* preferentially target individuals on the group periphery, which in this species happen to be males (Fitzgibbon 1990). Norrdahl and Korpimäki (1998) showed that radio-collared female field voles *Microtus agrestis* and sibling voles *Microtus rossiaemeridionalis* experience higher predation risk than males. Large predatory cichlids 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. Old elk *Cervus elaphus canadensis* (Wright et al. 2006) and old female bighorn sheep *Ovis canadensis* (Festa-Bianchet et al. 2006) experience higher predation risk than prime-age adults. In such cases, the higher selectivity for older animals is shaped by the prey behaviour: old elk are less able to escape after being coursed by wolves *Canis lupus*, while old female bighorn sheep travel ahead of the group and are thus more vulnerable to ambush by mountain lions *Puma concolor*. But higher selectivity for an age class can also be driven by the predator’s hunting abilities and physiological constraints. Red foxes *Vulpes vulpes* are unable to kill relatively large prey (perfectly illustrating the concept of “gape limitation”; Urban 2007), so young roe deer *Capreolus capreolus* progressively experience lower predation risk by foxes with increasing age (Panzacchi et al. 2008).

Other, less commonly thought of, phenotypic attributes might sometimes be involved (Table 1). For example, Thompson and Peterson (1988) suggested that differential cohort vulnerability to wolf predation may be traced back to food limitation and snow conditions during the first year of life in moose *Alces alces*. While comparing two boreal forest landscapes in Canada (namely, an old uncut landscape and a regenerating logged landscape), Andruskiw et al. (2008) showed that the frequencies of prey encounters, prey attacks, and prey kills by American martens *Martes americana* were higher in old uncut forests, despite

Table 1 Examples of phenotypic attributes structuring individual variability in prey susceptibility to predation

Prey species	Phenotypic attribute	Reference
Thomson's gazelle <i>Gazella thomsonii</i>	Sex	Fitzgibbon (1990)
Moose <i>Alces alces</i>	Year of birth	Thompson and Peterson (1988)
White-tailed deer <i>Odocoileus virginianus</i>	Mother's experience	Ozoga and Verme (1986)
Caribou <i>Rangifer tarandus</i>	Birth date	Adams et al. (1995)
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)
Field voles <i>Microtus agrestis</i>		Karell et al. (2010)
Bighorn sheep	Personality	Réale and Festa-Bianchet (2003)
Moose	Habitat	Berger (2007)
Elk		Hebblewhite et al. (2005)
House sparrow <i>Passer domesticus</i>	Body mass	MacLeod et al. (2006)
Snowshoe hare <i>Lepus americanus</i>	Body condition	Murray (2002)
Feral horse <i>Equus caballus</i>	Coat colour	Turner and Morrison (2001)

the fact that red-backed vole *Clethrionomys gapperi* density was similar to that in younger logged forests. These differences in predation efficiency were linked to higher abundance of coarse woody debris, which seems to offer sensory cues to martens, thereby increasing the odds of hunting success. Several studies across a range of taxa have then demonstrated that individuals can show consistent differences in aggressiveness, shyness, sociability and activity (Dall et al. 2004; Sih et al. 2004a, b). Such personality differences have been linked to variation in habitat use and predator avoidance tactics, ultimately impacting individual predation risk (Verbeek et al. 1996; Réale and Festa-Bianchet 2003; Boon et al. 2008).

Individual variability in indirect costs of predation

Again, theoretical and experimental research both suggest that (1) individuals from a population at a given time might not face the same costs linked to anti-predator tactics, and that (2) such inequality might be related to the fact that they do not face the same “average” lifetime indirect costs of predation, and/or to the fact that they do not face the same indirect costs of predation as they age. But is there evidence for such patterns in free-ranging vertebrates? The answer is yes, and again with evidence of both processes occurring. In elk, bulls display weaker anti-predator responses to wolf predation than cows, despite facing a greater risk of predation, suggesting that bulls are less able to pay the costs of higher vigilance in terms of lower foraging rates (Winnie and Creel 2007). Juveniles and yearlings spent more time looking up while feeding than did adult yellow-bellied marmots *Marmota flaviventris*, and juveniles were also reported to be more responsive to the factors that influence vigilance than were older animals (Carey and Moore 1986). Lion (*Panthera leo*) avoidance by female cheetah increases

with age, with older females found in areas of lower lion densities than younger ones (Durant 2000). While exploring responses of freshwater snails of the genus *Physa* to predation by crayfish *Orconectes rusticus* in the laboratory, Dewitt et al. (1999) demonstrated that small—and sometimes more vulnerable—prey can show stronger anti-predator behaviour than large ones (exhibiting behavioural compensation for morphological vulnerability). Habitat structure and the proportion of risky patches inside individual home ranges or territories can also influence indirect costs of predation: mule deer *Odocoileus hemionus* have, for example, higher giving-up densities (i.e. foraging costs due to predation risks; Brown 1988) along the edges of forests frequented by mountain lions than in open areas away from the forest (Altendorf et al. 2001). Red-backed voles in regenerating forest stands exhibited increased wariness compared to voles living in old uncut forest, suggestive of a behavioural response to habitat mediated variation in predation risk (Andruskiw et al. 2008). It is, however, unknown how these behavioural differences translate into differences in indirect costs of predation for these individuals. Finally, adult male Iberian rock lizards *Iberolacerta monticola* show consistent differences in the magnitude of their anti-predator responses under similar conditions of risk, and such differences were suggested to be linked to personality differences (Lopez et al. 2005).

Predators, prey selection, and individual differences

Prey selection and predation risk

While predation risk describes the link between predators and prey from the point of view of the prey, prey selection describes the link between predators and prey from the

point of view of the predators. Although they might sometimes describe two faces of the same coin (e.g. when preferred prey experience the highest predation risk), both are key to the understanding of predator–prey dynamics. Discrepancies in the information encapsulated by both parameters can occur; for example, when the indirect costs of predation are still high although individuals do not appear to be selected by predators (a situation which should occur when preferred individuals have become extremely good at avoiding predators; Creel and Christianson 2008). Like predation risk, prey selection tends to be shaped by a suite of factors, including predator and prey behaviour, morphology and habitat requirements related to hunting, escape or predation avoidance (Bakker 1983; Kruuk 1986). Prey selection can occur at different levels (e.g., selectivity for prey species, for prey size, for age or sex classes, and selectivity towards physically substandard individuals), and can be influenced by factors such as the presence of competitors, the number of individuals hunting (for social species), the habitat structure, or the season (e.g. Fitzgibbon and Fanshawe 1989; Mills and Gorman 1997; Kruger et al. 1999; Creel and Creel 2002; Pole et al. 2004; Radloff and du Toit 2004).

Optimal foraging and individual differences

As previously said, each prey item has particular associated costs and benefits to the predator, and the life history traits of predators are expected to be influenced by what they choose to eat (i.e. by their prey selection; Werner and Hall 1974). Because “smart” prey selection might lead to higher fitness, several authors have been trying to identify optimum tactics for predators in a given ecological situation, leading to the development of the “optimal foraging theory” (MacArthur and Pianka 1966). In its most basic form, optimal foraging theory states that organisms forage in such a way as to maximize their energy intake per unit time. Because prey selection occurs under given environmental conditions (and thus given costs and benefits associated with each prey item), one might expect individual variation in prey selection by predators. For example, risk-sensitive foraging behaviour can result in context-dependent optimal tactics (MacNamara and Houston 1992), and state-dependent models, in which the current condition of the forager affects its decisions, predict intrapopulation variation in predator diet (MacNamara and Houston 1986). The level of individual specialization was for example reported to fluctuate with perch *Perca fluviatilis* population density through feedback mechanisms via resource levels (Svanback and Persson 2004). After controlling for such factors, however, long-term individual differences in diet have been found to be quite common (Bolnick et al. 2003; Estes et al. 2003), and it has become

clear that individual specialization is much more common than once suspected (Estes et al. 2003).

Individual variability in prey selection, predator efficiency and its correlates

Are free-ranging vertebrate predators equal in terms of prey selection and predatory performance? Optimal foraging theory predicts individual variability in prey selection, a prediction largely supported by empirical data. Populations of predators in the wild indeed rarely consist of individuals with consistent, identical preferences for particular types of prey, and phenotypic attributes of predators such as age (Rutz et al. 2006; Field et al. 2007), sex (Cooper et al. 2007), reproductive status (Pierce et al. 2000), group size (Packer et al. 1990), family structure (Gaydos et al. 2005; Maniscalco et al. 2007) or social status (Saulitis et al. 2000) are all factors that can affect a predator’s diet (Table 2). Female mountain lions with offspring, for example, preferentially select female deer, while males and females without offspring do not (Pierce et al. 2000). Because age and size correlate in many predator species, and because predator gape size can correlate with prey size (Persson et al. 1996), age can sometimes strongly determine prey selection: larger blind snakes *Ramphotyphlops nigrescense* prey on large bulldog ants *Myrmecia* spp. while juvenile blind snakes are unable to do so (Webb and Shine 1993). In social predators, group size, composition and location might matter when it comes to prey selection: in the Serengeti, small groups of lions have been reported to be unable to kill buffalos *Syncerus caffer*, yet the species is an important prey item for larger lion prides (Packer et al. 1990; Scheel and Packer 1991). Likewise, factors such as age (MacNulty et al. 2009) or group size (Fryxell et al. 2007) are also factors that have been shown to affect predatory performance. In wolves, for example, an increasing ratio of senescent individuals has been shown to correlate with a depressed rate of prey offtake (MacNulty et al. 2009). Individual variability in prey selection has sometimes been reported without any obvious correlation with phenotypic attributes: neighbouring kestrels *Falco tinnunculus* were reported to show consistent differences in prey selection (with seven pairs feeding primarily on lizards while three preyed mostly on small birds), even though the birds were sharing the same hunting grounds (Costantini et al. 2005).

Where to go from there? Implications, opportunities and future work

Our review suggests that (1) individual variability in predation risk and indirect costs of predation are common in

Table 2 Examples of phenotypic determinants of individual specialization in prey selection by predators

Predator species	Phenotypic determinant	Reference
Cougar <i>Puma concolor</i>	Age	Ross et al. (1997)
Cheetah <i>Acinonyx jubatus</i>	Sex	Cooper et al. (2007)
Cormorant <i>Phalacrocorax carbo</i>	Age and sex	Stewart et al. (2005)
Cougar <i>Puma concolor</i>	Reproductive status	Pierce et al. (2000)
Lynx <i>Lynx lynx</i>		Nilsen et al. (2009)
Blood python <i>Python brongersmai</i>	Colour	Shine et al. (1998)
Darwin's finches <i>Geospiza fortis</i>	Bill size	Price (1987)
Oystercatcher <i>Haematopus ostralegus</i>	Dominance/social status	Sutherland et al. (1996)
Killer whale <i>Orcinus orca</i>		Saulitis et al. (2000)
American robin <i>Turdus migratorius</i>	Body size	Jung (1992)
American pine marten <i>Martes americana</i>	Territory location	Ben-David et al. (1997)
Lion <i>Panthera leo</i>	Dental problems	Baldus (2006)

free-ranging vertebrates, and that these differences can in part be associated with prey phenotypic attributes, (2) individual variability occurs in prey selection and predatory performance, and (3) part of the individual predator's specialization and efficiency can be linked to its phenotypic attributes. From an evolutionary and population dynamic point of view, this raises several questions and opportunities for future research.

- (1) Does the presence of predators lead to differences in the means and variation in survival and recruitment rates among phenotypic categories within a free-ranging prey population?

Although largely explored theoretically, in laboratory systems or in invertebrates (Relyea 2002, Bronikowski et al. 2002, Kunert and Weisser 2003, Fisk et al. 2007), we still lack information regarding the importance of predation in shaping life history traits of free-ranging vertebrates (especially terrestrial vertebrates; but see e.g. Coltman et al. 2003 for an illustration of the importance of selective harvesting in shaping life history traits of free-ranging vertebrates). This is well exemplified by the difficulty of demonstrating the importance of indirect costs of predation on vertebrate prey population dynamics (Creel and Christianson 2008). Results suggest that the effect of predators on prey life history traits are a function of the type of predation, the predation pressure, the length of time with predators and prey coexisting and prey population state and dynamics, with populations facing predation occurring at lower density (leading to changes in the effects of density dependence) than populations without predators when everything else (resources and climate in particular) is set constant (Bronikowski et al. 2002; Kunert and Weisser 2003; Fisk et al. 2007). In that context, the re-colonization of many ecosystems by large predators provides an interesting natural

setting to gather information, and future research should consider such effects when assessing the impact of predators on prey.

- (2) Why is individual variability in predator diet important?

Individual dietary variation is expected to have broad ramifications for population and community dynamics. First, dietary differences can act to reduce competition among individuals within a population of predators. This was demonstrated by Svanback and Bolnick (2007), who showed that increased population density of three-spine sticklebacks *Gasterosteus aculeatus* led to reduced prey availability, causing individuals to add alternative prey types to their diet. Second, individual variability in the selective behaviour of the predators might lead to predation risk and costs of anti-predator tactics being spatially variable across prey populations ("landscape of fear"; Laundré et al. 2001), depending on the spatial distribution of the individual predators with particular specializations. Such an effect might contribute to increasing the role of spatial variation in prey life history traits in determining prey population dynamics. Lastly, neglecting behavioural variation in prey selection by predators while modelling prey population dynamics can lead researchers and managers to overestimate or underestimate the expected impacts of predators on prey populations (Okuyama 2008; Karell et al. 2010).

A good example is provided by individual mountain lions specializing on bighorn sheep (Festa-Bianchet et al. 2006): reducing mountain lion densities at large scales might have little effect on reducing predation pressure on bighorn sheep (if the specialized individuals are missed by the predator control program) while affecting the overall predators' population structure and functioning (Robinson et al. 2008).

- (3) Do changes in the average composition (i.e. age and sex structures, group size) of the predator population lead to differences in the means and variation in survival and recruitment rates among phenotypic categories within a free-ranging prey population?

Does the existence of individual variation in predators' diet and hunting efficiency really matter from a prey population dynamic point of view? Is this worth considering when modelling predator and prey population dynamics in free-ranging populations? Investigating such questions necessitates close monitoring of both prey and predator populations over a sufficient time frame. Unfortunately, most long-term projects on large vertebrate populations have been carried out in predator-free environments, reducing opportunities to empirically address this question. Where such an investigation is possible, recent work suggests that inter-individual differences can affect predator impacts on prey (MacNulty et al. 2009). Other options for exploring this issue might include experimentation (Bonsall and Hassell 2005) and simulation work (Okuyama 2008).

- (4) Are predator species characteristics influencing the level of individual variability in predator diet?

A study across five taxa provided evidence that generalist populations exhibit more niche variation than specialist populations, leading to the conclusion that ecological generalists, which use a wide diversity of resources, could in fact be heterogeneous collections of relatively specialized individuals (Bolnick et al. 2007). However, Sinclair et al. (2003) reported that the range of available prey for a predator species is a function of its size, with larger predators preying upon a wider range of species. The same association between niche breadth and body size was reported for insects (Wasserman and Mitter 2008), but could not be found in fish (Unger and Lewis 1983), predatory lizards (Costa et al. 2008), or within a carnivore community (as opposed to Sinclair et al. 2003; see Durant et al. 2010). If larger species tend to be more generalist, then higher individual variability in prey selection would be expected in larger predators. If this is correct, then considering individual variability in predator diet should be particularly relevant when modelling population dynamics of prey facing predation by relatively large species.

Conclusion

Predator–prey interactions have fascinated behavioural ecologists, population ecologists and evolutionary biologists for more than a century, yet many challenges are still

ahead, challenges which will need the development of multi-disciplinary, integrated projects to be properly tackled. Understanding the population dynamic consequences of predation clearly requires more information than simply how many individuals are killed by predators, or what the proportion of prey killed by predators is, and evidence is accumulating regarding the importance of individual variability in structuring predator and prey behaviour, life history parameters and population dynamics. In particular, our review suggests that individual variability in predation risk, indirect costs of predation, prey selection and predatory performance is common in free-ranging vertebrates, and that these differences may be associated with predator and prey phenotypic attributes.

Although evidence is clearly accumulating, our work reveals several shortcomings in the information currently available that is relevant to the exploration of individual variability in predation risk, predation costs and prey selection in the wild: not only are studies on the topic rare, but these studies need to be evaluated critically with respect to limitations in sample size, lack of replication across different study areas, and interpretation of data or possible explanations behind the observed patterns. For example, we illustrated age-related individual variability in indirect costs of predation with observations that juveniles and yearlings spent more time looking up while feeding than did adult yellow-bellied marmots (Carey and Moore 1986): this example assumes that (1) the observed difference in behaviour translates into differences in energetic costs for the age classes considered, and (2) predation risk is the variable driving this difference in behaviour.

As demonstrated throughout this review, there is (1) a clear lack of longitudinal studies that have the potential to disentangle the relative importance of various phenotypic attributes in shaping individual variability in prey selection, predation risk and predation costs, (2) a general difficulty when it comes to reliably indexing these parameters, as well as (3) a lack of studies exploring the physiological mechanisms behind individual variability in these parameters. We consequently believe this work highlights the importance of (1) maintaining long-term, detailed studies of individuals of both predators and prey in contrasted ecological conditions to provide information on the importance and the factors structuring individual variability in predation risk and costs associated with anti-predator tactics, and (2) making a better use of the available modelling framework to account for such effects. Future strides in our understanding of these complex relationships might be particularly aided through the combined use of modelling and experimentation.

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