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Experimental size- and sex-specific predation on dung flies by amphibian and arthropod predators

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Abstract

Because predator-prey interactions in nature are multifarious, linking phenomenological predation rates to underlying behavioral or ecological mechanisms is challenging. Size- and sex-specific predation has been implicated as a major selective force keeping animals small, directing the evolution of body size and sexual size dimorphism. We experimentally assessed predation by 4 amphibian and 3 arthropod species (bug, fly, spider) on 3 species of dung flies with similar ecology but contrasting body sizes, sexual size dimorphism, and coloration. Predators were offered a size range of male and/or female individuals of one prey species. As expected based on optimal foraging theory, some anurans (*Bufo bufo*) preferred larger prey individuals, others (*Bombina variagata*, *Rana esculenta*) showed no preference. Small juvenile *Rana temporaria* metamorphs preferred small prey, as did all arthropod predators, a pattern that may be explained by gape limitation or larger prey escaping better. Presumably more mobile males were not preyed upon more frequently or faster than cryptic females, even when conspicuously colored. Contrary to expectation, predation rates on flies in mixed groups facilitating mating activity were not higher, nor was predation generally sex-specific, hence contributing little to sexual dimorphism. We conclude that the size-selectivity of predators, and hence the viability selection pattern exerted on their prey, depends foremost on the relative body sizes of the two in a continuous fashion, in addition to any specific prey defense mechanisms. Therefore, the mechanistic study of predation requires integration of both the predator and prey perspectives, and phenomenological field studies of predation remain indispensable.

1 **Introduction**

2 Predation is a fundamental ecological process that plays a central role in the evolution of animal
3 life histories and affects most if not all species (Roff, 1992). As such predation features
4 prominently in life history optimality (e.g. Stearns & Koella, 1986; Fraser & Gilliam, 1992;
5 Kozlowski, 1992; Werner & Anholt, 1993; Abrams *et al.*, 1996; Leimar, 1996; Ruxton *et al.*,
6 2004) as well as food web and functional response theory (Kalinkat *et al.*, 2011, 2013). For
7 instance, in Trinidadian guppies variation in predation pressure in natural streams mediates
8 variation in extrinsic mortality rates that ultimately leads to the evolution of earlier maturity,
9 often at smaller size, and altered reproductive schedules (e.g. Reznick *et al.*, 2004). In the same
10 species, predation pressure (i.e. viability selection) by optically oriented fish balances advantages
11 large males with colored spots have when mating (i.e. sexual selection; Endler, 1980). Though
12 ubiquitous, predation is not easily assessed beyond the traditional, somewhat crude food web
13 perspective, which historically treated interspecific predatory relationships mainly in terms of
14 presence or absence (i.e. who eats whom: Cohen *et al.*, 1993; Brose, 2010). A major problem is
15 that most predators, contrary perhaps to many parasitoids (e.g. Stireman & Singer, 2003;
16 Sandrock *et al.*, 2011), are typically not very specialized on particular prey species (Symondson
17 *et al.*, 2002; Ruxton *et al.*, 2004; Scherer & Smee, 2016). That is, predator-prey interactions in
18 nature are necessarily multifaceted, typically involving complex interactions among many prey
19 and many predator species, which additionally depend on habitat characteristics, ecological
20 context, body size, or taxonomic group, to only name the most obvious factors. Consequently, it
21 is often difficult to link the phenomenological predation rate estimates needed for e.g. functional
22 response curves of particular predator-prey interactions to the underlying behavioral mechanisms
23 (e.g. specific predator evasion behavior, or chemical defense) or ecological circumstances (i.e.

1 population size, community composition, etc.; Kalinkat *et al.*, 2011, 2013), as called for by
2 Blanckenhorn (2000, 2005) when reviewing experimental studies of viability selection. This in
3 turn is problematic for generating realistic estimates for predictive ecological models in
4 theoretical and applied contexts (Kalinkat *et al.*, 2011; Rummel *et al.*, 2011). An eco-
5 evolutionary functional trait approach, as it is now called (Weiss & Ray, 2019), may provide a
6 solution.

7 Size- and sex-specific predation has been implicated as a major selective force keeping
8 animals small because most predators should prefer large prey, thus directing the evolution of
9 body size and sexual size dimorphism of many organisms (Blanckenhorn, 2000, 2005;
10 Kingsolver & Pfennig, 2004). Whereas sexual and fecundity selection typically favor larger
11 males and females of a given species, unequivocal evidence of counterbalancing selective forces
12 disfavoring large body size is still lacking (e.g. Endler, 1980). If a majority of predators had
13 reported preferences for larger prey, this problem might be solved. Importantly in this context,
14 mortality risk of most animals is mediated by behavior in many contexts at any life stage: the
15 hunting behavior of the predator, the evasion behavior of the prey, or the foraging behavior of
16 either necessary to avoid starvation (Ruxton *et al.*, 2004; Blanckenhorn, 2005). Optimal foraging
17 theory postulates and documents that predators should be sensitive to the energy content and size
18 of their prey (Stephens & Krebs, 1986; Sih & Christensen, 2001). On the other hand, at one point
19 prey become too big or strong for any given predator, consequently requiring excessive handling
20 time; or the prey might no longer fit into the predator's mouth (the concept of gape limitation:
21 e.g. Truemper & Lauer, 2004). Both effects imply an optimal prey size in terms of profitability
22 (i.e. energy obtained relative to energy invested: Stephens & Krebs, 1986; e.g. Elner & Hughes,
23 1978). Therefore, a rough positive correlation between predator and prey size and, globally,

1 intermediate predator-prey size ratios are expected (Brose *et al.*, 2006). Taking the prey
2 perspective, however, studies often find viability advantages of larger individuals, rather than the
3 expected disadvantages based on optimal foraging of the predator (Blanckenhorn, 2000, 2005).
4 This relates to some extent to the hypo-allometric scaling of metabolic rate (e.g. Reim *et al.*,
5 2006; Blanckenhorn *et al.*, 2007), but surely also involves gains in strength aiding larger prey in
6 escaping predation. Moreover, as they transition through life stages, growing prey will likely
7 consecutively pass through the optimal size windows of various predators of ever larger size,
8 facing predation risk at most times (Wellborn, 1994; Berger *et al.*, 2006; Mänd *et al.*, 2007;
9 Remmel *et al.*, 2011). It follows that the mechanistic and functional study of predation requires
10 integration of both the predator and prey perspectives, though even when doing so might never be
11 complete because the entire spectrum of species involved cannot possibly be covered.

12 Intra-specific experimental studies of sex- and size-selective predation are uncommon but
13 exist in the literature. The topic seems to be of more interest in aquatic (fish, cladocerans,
14 tadpoles, etc.) than terrestrial organisms (e.g. Sogard, 1997; Scherer & Smee, 2016). Terrestrial
15 investigations in the functional response and food web contexts concentrate on soil invertebrates
16 (Kalinkat *et al.*, 2013), but are typically phenomenological in frequently ignoring crucial
17 behavioral traits (but see Vucic-Pestic *et al.*, 2010; Kalinkat *et al.*, 2011, for good
18 counterexamples). Remmel *et al.* (2011) reviewed predation on holometabolous insect (primarily
19 butterfly) larvae feeding on plant leaves (folivory) to find that birds preyed predominantly on
20 larger larvae, while arthropod predators rather preferred smaller prey (see also Sogard's (1997)
21 review for marine fish). This result emphasizes that when taking the predator perspective, we
22 may obtain a clear pattern, but when taking the prey perspective, net selection on body size may
23 well turn out to be unrelated to size because typically multiple predators prey on the same

1 species, some of which will prefer small and others large individuals (e.g. Luning, 1992; Rice *et*
2 *al.*, 1993).

3 Apart from body size, the sex of the prey should also matter. Even when of the same size,
4 males and females of a given species can behave very differently, ultimately affecting their
5 probability of being preyed upon. For example, predation risk has been found to be greater for the
6 sex attracting mates via acoustic or visual signals, or for the sex that has to move more or farther
7 to find mates. Thus, the sex competing more for mates, typically males, frequently faces greater
8 predation risk or energy expenditure when searching (Slagsvold *et al.*, 1988; Magnhagen, 1991),
9 attracting (Partridge & Farquhar, 1981; Lima & Dill, 1990; Cordts & Partridge, 1996; Kotiaho *et*
10 *al.*, 1998; Zuk & Kolluru, 1998), assessing (Pomiankowski, 1987; Hedrick & Dill, 1993), or
11 rejecting potential mates (Rowe, 1994; Watson *et al.*, 1998; Jormalainen *et al.*, 2001). Moreover,
12 the act of mating itself, or that of avoiding mating, should also increase predation rates, if only
13 because a mating pair attracts more attention, is more visible, and/or less mobile (Magnhagen,
14 1991; Mühlhäuser & Blanckenhorn, 2002). It is therefore likely that sex and body size interact in
15 determining the outcome of predation, for instance if large prey individuals are more likely to
16 mate (which is common), if there is size-assortative mating, or if predators systematically eat
17 only one of the mating partners because of its position (Teuschl *et al.*, 2010).

18 Pastoral grasslands are ubiquitous habitats harboring a large array of interacting species
19 that typify the agricultural landscape of many developed countries. We here investigate predation
20 on three of the most abundant and widespread dung flies in Europe with similar ecology but
21 contrasting body sizes, sexual size dimorphism and coloration (i.e. conspicuousness; Pont &
22 Meier, 2002; Blanckenhorn *et al.*, 2010). Yellow dung fly (*Scatophaga stercoraria*) males are
23 bright yellow to orange, hairy and on average considerably larger than the greenish, more cryptic

1 females. *Sepsis cynipsea* males are smaller than females, and both are shiny black; *S. thoracica*
2 males feature an additional male dimorphism with large orange and small black males, and black
3 females of intermediate size (Busso & Blanckenhorn, 2018a,b). All these flies lay their eggs into
4 cow dung, in which the larvae develop. Their mating behavior around the dung of livestock
5 (primarily cows) is characterized by scramble and contest competition of males for access to
6 females, with at times conspicuous mate rejection and struggle behavior, and relatively long
7 copulation and guarding durations (20 – 60 min: Parker, 1970, 1972; Ward, 1983; Ward *et al.*,
8 1992; Blanckenhorn *et al.*, 2000; Jann *et al.*, 2000). All dung fly species also spend considerable
9 time foraging for nectar and insect prey (*Sc. stercoraria* only) in the vicinity of pastures
10 (Warncke *et al.*, 1993), forested or not. Accordingly, in addition to various specialized predators
11 of juvenile stages in and around the dung (Hammer, 1941; Skidmore, 1991; Pont & Meier, 2002),
12 adult dung flies regularly face a large guild of generalist predators in their habitat. These include
13 vertebrates such as various insectivorous birds, *Lacerta* lizards, and several amphibians where
14 ponds and streams are common, but also many invertebrates, primarily jumping, crab and orb-
15 weaver spiders, and predatory insects (wasps, scorpion flies, bugs, various dipterans including
16 adult *Sc. stercoraria* itself, etc.; Hammer, 1941; Skidmore, 1991). No systematic assessment of
17 this predator guild is available.

18 We here report standardized assessments of predation on common dung flies by a number
19 of amphibian and insect predators. Our main aim was to integrate multiple semi-natural but
20 realistic predation assessments of various typical predator and prey species to obtain an overall
21 estimate of size- and sex-specific predation for terrestrial grasslands from the (dung fly) prey
22 perspective. Our selection of predators and prey was necessarily idiosyncratic and incomplete,
23 however should be sufficiently representative for the pastoral habitat considered. We expected

1 that the larger vertebrate predators (mostly anurans) would prefer larger prey when feeding on
2 relatively small flies so as to optimize their energy gain, whereas the smaller arthropod predators
3 (bugs, flies, spiders) would rather select smaller individuals (if selective at all) because larger
4 prey require prohibitive handling (Brose *et al.*, 2006; Rimmel *et al.*, 2011). We further expected
5 the more mobile and often more colorful males to be subject to greater predation than the cryptic
6 females, and flies in a mixed setting permitting mating activity to be subject to greater predation
7 than in single-sex groups (Rimmel & Tammaru, 2009; Svanbäck & Eklöv, 2011; Teuschl *et al.*,
8 2010).

10 **Materials and Methods**

11 *Prey species*

12 As prey, we used three species of dung flies: the yellow dung fly *Scathophaga stercoraria*
13 (Diptera: Scathophagidae) plus two black scavenger (or ensign) fly species, *Sepsis cynipsea* and
14 *S. thoracica* (Diptera: Sepsidae). The sepsids are primarily black and considerably smaller than
15 scathophagids (6 – 13 vs. 3 – 9 mm in length; 8 – 48 vs. 0.5 – 3.6 mg in wet mass). The first two
16 species are the most common dung flies in north-central Europe and have been used extensively
17 as models in evolutionary ecology (e.g. Blanckenhorn, 2007; Blanckenhorn *et al.*, 2010; see
18 <http://sepsidnet-rmbr.nus.edu.sg/> for pictures). *Sepsis thoracica* is the most common sepsid fly
19 around livestock dung in the Mediterranean parts of Europe, but is also frequent north of the Alps
20 (Pont & Meier, 2002; Busso & Blanckenhorn, 2018b).

21 Prey flies used in this experiment all stemmed from laboratory cultures held in groups
22 (sepsids) or individually (*Sc. stercoraria*) in plastic or glass containers under standard conditions
23 with water, sugar as food, and cow dung as food and oviposition substrate (see Blanckenhorn *et*

al. 2000, 2010, for details). To obtain a broad range of prey body sizes, the phenotypic size of the flies was manipulated by raising them at various dung (i.e. food) quantities and/or population densities. The hind tibia length of all prey individuals as determined under a binocular microscope served as an estimate of their body size. All prey individuals were used only once.

Vertebrate predators

As vertebrate predators, we used a number of amphibian species of various sizes common in Swiss grasslands. In general, we collected predator individuals ourselves around Irchel campus, a typical pasture habitat close to forest featuring some ponds and streams (47.40°N, 8.55°E). Some predators stemmed from experimental populations colleagues held on campus. Standard snout-vent-length (SVL) of all predators was used to estimate their size, using calipers. Amphibian predators were held in 1.3 x 1.3 x 1.8 dm³ plastic containers (cf. below) and used more than once. In the laboratory, we occasionally fed predators at need with a mix of *Drosophila* species (*D. melanogaster*, *D. virilis*, *D. americana*, *D. novamexicana*), while trying to keep them hungry. At the end of our experiments, predators were released into the wild where originally captured.

We originally attempted a crossed experimental design in confronting all predators with both *Sc. stercoraria* (large prey) and *Se. cynipsea* (small prey; *Se. thoracica* data were added later, see below). However, most amphibian predator species ate only one or the other prey species, and the marsh frog *Rana ridibunda*, the Alpine newt *Ichthyosaura* (formerly *Triturus*) *alpestris*, or the fire salamander *Salamandra salamandra* did not produce usable data sets for either prey species in captivity. Complete data sets with at least ten replicates per sex treatment (explained below) were obtained for the common toad *Bufo bufo* (4 predator individuals, size range 55 – 82 mm SVL; predation experiments with *Sc. stercoraria* and *Se. cynipsea*), the

1 yellow-bellied toad *Bombina variegata* (11 individuals, size range 26.9 – 37.7 mm SVL; *Sc.*
2 *stercoraria* only), the edible frog *Rana esculenta* (now *Pelophylax esculentus*; 8 individuals, size
3 range 58 – 74.5 mm SVL; *Sc. stercoraria* only), and juveniles of the common frog *Rana*
4 *temporaria* (4 individuals, size range 13.6 – 14.7 mm SVL; *Se. cynipsea* only; Table 1). All these
5 amphibians are mainly sit-and-wait predators but also actively orient towards moving prey.

6 7 *Arthropod predators*

8 As arthropod predators are small relative to their prey, we only used sepsids as prey for them.
9 (While *Sc. stercoraria* would cannibalize individuals of its own species regularly, the other two
10 predators did not regularly manage to catch prey this large.) We in the end selected three
11 arthropod predators differing by taxonomic group, body size and hunting technique, after
12 verifying in the field that they in fact prey on sepsids: the jumping spider *Heliophanus flavipes*
13 (Areanae: Salticidae), an active hunter 5 – 13 mm in total length; the damsel bug *Himacerus*
14 *mirmicoides* (Heteroptera: Nabidae), a sit-and-wait predator 11 – 15 mm long; and the predatory
15 yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae), a sit-and-wait but also
16 active hunter 6 – 12 mm long. Predation experiments with *Sc. stercoraria* as predator and *Se.*
17 *cynipsea* as prey were performed around the time of the experiments with amphibian predators
18 described above (cf. Teuschl *et al.*, 2010), whereas those using the arthropod predators and *Se.*
19 *thoracica* were carried out later.

20 The spiders and bugs, many of them juveniles, were collected around Irchel campus and
21 subsequently maintained individually in 1 x 1 x 1.4 dm³ plastic containers in the laboratory (cf.
22 below). After capture, we fed juvenile predators in the laboratory with water and a mix of
23 *Drosophila* species (*D. melanogaster*, *D. virilis*, *D. americana*, *D. novamexicana*) at need; they

1 were starved once they reached adulthood. *Sc. stercoraria* individuals (with dung-feeding larvae)
2 were raised in the laboratory as described above. Only adult female arthropods were used as
3 predators (because they are more voracious), merely once.

4 5 *Size-dependent predation experiments*

6 To investigate size- and sex-dependent predation, we set up single-sex and mixed-sex groups of
7 flies of varying body sizes. We examined 10 – 28 replicate groups per predator and sex treatment.
8 In the experiments with amphibian predators, we randomly assigned 10 males, 10 females, or 5
9 male plus 5 female (in the mixed-sex case) prey individuals of various sizes (gauged by eye) into
10 a transparent 1.3 x 1.3 x 1.8 dm³ experimental container. Because all amphibians swallow their
11 prey whole, all flies were measured before the experiment, and only the surviving flies were
12 measured again thereafter (to match individuals and calculate selection coefficients).

13 In the experiments with arthropod predators and male *Se. thoracica* as prey, we assembled
14 3 (large) orange plus 3 (small) black males into smaller 1 x 1 x 1.4 dm³ transparent experimental
15 containers. The corresponding mixed-sex treatment consisted of 4 males plus 4 females, whereby
16 10 replicates featured only large orange males, 10 only small black males, and 10 both orange
17 and black males (2 + 2). No female only treatment was conducted with *Se. thoracica* as prey
18 because we were primarily interested in the effect of coloration at this point (see Busso &
19 Blanckenhorn, 2018a). In the experiment with *Sc. stercoraria* preying upon *Se. cynipsea*, 16 prey
20 individuals were used in the above-mentioned larger containers (Teuschl et al. 2010). All
21 arthropod predators digest their prey externally, leaving the entire exoskeleton behind, so prey
22 size could be measured after the experiment.

23 All test containers were provided with water, sugar, pollen and fresh cow dung, plus a

1 natural structure (plant leaf, branch, etc.) as potential shelter for the predators and the prey. For
2 the anuran predators, we additionally added half a plant pot as shelter, a water dish, and a layer
3 (ca. 2 cm) of humidified commercial plant soil. In each replicate, the prey flies were released into
4 the test containers first and given at minimum 15 min to accommodate. The predator was added
5 thereafter, marking the beginning of the experimental period. Predators had been starved at least
6 during the day they were used in an experimental trial, often the day before as well, so as to be
7 hungry. Experimental replicates were stopped when approximately half of the flies were eaten,
8 and the time this took was noted. This temporal calibration of the experiment was necessary
9 because the predators varied strongly in how fast they ate their prey depending on species, hunger
10 level, etc., and because selection coefficients cannot be computed if none or all prey survived.

12 *Statistical analysis*

13 We used the methods of Arnold & Wade (1984) for dichotomous fitness measures (dead/alive =
14 1/0) to estimate standard selection coefficients. For each prey group, all tibia lengths (x) were
15 first z -scored as $z_i = (X_i - \text{mean}(X)) / SD(X)$, thus standardizing mean and variance. In the mixed
16 sex groups females and males were z -scored separately because of size dimorphism (Teuschl et
17 al. 2010). The selection differential is then simply equal to the mean standardized body size of
18 the surviving flies (because the pre-selection mean was set to zero). Note that this standardization
19 works equally for any (linear) size metric, and that the total number of prey, and their size range
20 within the group, both of which here varied depending on predator, prey, treatment, and container
21 size, only affects the precision of the selection differential but does not bias the estimate, thus
22 permitting direct comparisons of naturally varying group sizes and species (Arnold & Wade,
23 1984).

The resulting selection differentials (one per replicate container) were analyzed as outcome variables using general linear models with predator and prey species, treatment (females only, males only, mixed sex), and sex within treatment as fixed factors. For the amphibians that were used repeatedly, (the size of the) predator individual was additionally entered as random effect. In such models the intercept can serve to test for consistent selection across treatments, predator and/or prey species (cf. Fig. 1).

In the end, overall predation selection differential averages per predator/prey species combination (N=9) were computed across all treatment combinations varying by prey sex, which were plotted against the size ratio of predator/prey.

Results

Amphibian predators showed variable size selectivity with regard to the fly prey offered. In contrast, the three arthropod predators generally consumed more small flies, thus overall exerting positive viability selection (Fig. 1). The 95% confidence intervals ($= 1.96 \cdot \text{SE}$ for z-scored data) of many mean selection differentials overlap zero in Fig. 1, indicating no significance. Overall significant negative viability selection (i.e. negative selection differentials), equivalent to predators disfavoring large prey size, was exerted only by the toad *Bufo bufo* on both *Sc. stercoraria* and *Se. cynipsea* (significant intercepts in the separate models including all treatments (females, males, mixed): $F_{1,96} = 10.20, p = 0.002$ and $F_{1,54} = 24.52, p < 0.001$, respectively; Fig. 1c,e). Overall significant positive selection (i.e. positive selection differentials), equivalent to predators favoring large prey flies, was exerted by *Rana temporaria* juveniles on *Se. cynipsea* ($F_{1,52} = 5.90, p = 0.019$; Fig. 1d), and by *Sc. stercoraria* on *Se. cynipsea* ($F_{1,36} = 5.71, p = 0.022$; Fig. 1f). Importantly, these selection results did not vary across the various treatments involving

prey sex (females only, males only, or mixed groups) for any single species pair, or overall ($p > 0.2$); nor did they vary with amphibian predator identity (random effect when repeatedly used).

Figure 2 clearly demonstrates that the overall mean predator/prey size ratio (using total body length for arthropods and SVL for amphibians) is a crucial parameter influencing prey selection by predators (cf. Brose et al., 2006): the smaller the size difference between the two interacting species, the stronger the relative viability advantage of large prey individuals, presumably primarily due to the increased handling time associated with their capture (Stephens & Krebs, 1986).

Considering only the mixed-sex treatments, we found that there was no consistent sex bias in selection on the various dung fly prey species across the diverse predators (non-significant intercept of overall model: $F_{1,113} = 1.06, p = 0.308$): *Rana temporaria* juveniles took significantly more male *Se. cynipsea*, while *Sc. stercoraria* took more female *Se. thoracica* (Fig. 3); all other predators did not show any prey sex bias. The latter result was unexpected given that the orange *Se. thoracica* males were deemed much more conspicuous.

Discussion

Our study revealed a systematic preference of three different arthropod predators (spider, bug, fly) for smaller black scavenger flies *Se. cynipsea* and *Se. thoracica*, thus exerting positive directional viability (i.e. predation) selection on the body size of the prey. In contrast, the four amphibian predators (frogs and toads) showed variable prey selection: the common toad *Bufo bufo* preferred to capture larger flies of two species, thus exerting negative predation selection, whereas the small common frog (*Rana temporaria*) metamorphs consumed more small flies, while the two other species tested were non-selective (Fig. 1). We had generally expected

1 preference of large prey by the large predators (not only *Bufo bufo*), based on optimal foraging of
2 energetically more profitable prey with at the same time reduced handling times (Stephens &
3 Krebs, 1986; Sih & Christensen, 2001; Brose *et al.*, 2006; Vucic-Pestic *et al.*, 2010), but this did
4 not happen. At the same time, we expected and indeed found that smaller (arthropod) predators
5 would catch more small prey, presumably because larger prey should be more effective in
6 escaping or fending off relatively small predators, thus requiring excessive handling by the
7 predator, which however was not assessed here. It is also possible that larger prey move more
8 quickly, thus at one point setting a threshold to the ability of a predator to capture them.

9 Alternatively, smaller prey individuals might be more mobile, hence more easily detected and
10 eaten by predators (Mühlhäuser & Blanckenhorn, 2002). However, this is unlikely here (and was
11 not measured) because of lacking differences among the prey sex treatments (Figs. 1, 3), and lack
12 of size dependence of *Se. cynipsea* mobility in a previous study (Teuschl *et al.*, 2010). Moreover,
13 most if not all sepsid flies are known to release a substance smelling like geraniums suggested to
14 be a chemical deterrent against predators (Pont & Meier, 2002). We know that when given a
15 choice, *Sc. stercoraria* prefers *Drosophila* over *Sepsis* prey (of roughly the same size;
16 unpublished data). Should larger individuals release more deterrent substances, which to date is
17 unknown, this could have contributed to larger prey flies being eaten less, especially by the small
18 arthropod predators. Another aspect not properly controlled here is predator satiation, as at least
19 the amphibian predators were used repeatedly and therefore sporadically fed in the laboratory.

20 However, this merely introduces surplus variation but no systematic bias, as this aspect would
21 mainly affect the speed at which individual predators capture prey – provided they eat the offered
22 prey at all – which was not controlled by our methods because we stopped each trial when
23 approximately half the prey was eaten (see Methods). Overall, then, various mechanisms may

1 explain idiosyncratic prey size preferences of some or the amphibian predators tested here, but
2 this must remain inconclusive. Thus, our admittedly limited study (in terms of species) confirms
3 our intuition that size- and sex-specific predation varies unpredictably, such that overall net
4 selection on the size of any given prey species cannot be reliably estimated from such behavioral
5 predation experiments, because they will never be complete (enough) in practice (cf.
6 Blanckenhorn, 2000, 2005).

7 The above-mentioned trade-off involving prey profitability and handling time here
8 predicted opposite size-selectivity of large vs. small predators, but can theoretically result in any
9 intermediate pattern. When plotting predation selection as a function of the predator/prey length
10 ratio (cf. Vucic-Pestic *et al.*, 2010), we indeed found a continuous shift from positive (for
11 relatively small predators) to negative selection (for relatively large predators; Fig. 2), suggesting
12 that the profitability aspect becomes increasingly dominant as predators increase in size.
13 Admittedly, our relative range in prey size was much smaller than the range in predator size
14 (Table 1). A contrasting argument predicts less selectivity as predators grow larger (relative to
15 their prey) simply because they can eat a wider variety of prey (Schmitt & Holbrook, 1984),
16 which however is not supported by the selectivity pattern found here (Fig. 2). Our study generally
17 supports similar patterns found for herbivorous insect (mainly butterfly) larvae eaten by
18 arthropods (exerting largely negatively size-dependent selection) or birds (often exerting
19 positively size-dependent selection: Remmel *et al.*, 2011). While omitting bird predators entirely,
20 we here focused on various common sit-and-wait amphibian and arthropod predators of
21 widespread dung flies in pastoral grasslands, a common human-influenced environment very
22 different from the typically forested habitats covered by Remmel *et al.* (2011).

23 Foraging theory postulates an optimal prey size in terms of profitability (i.e. energy

1 obtained relative to energy invested: Elner & Hughes, 1978; Stephens & Krebs, 1986), as at one
2 point the prey becomes too big or strong for a given predator, involving too much handling, or
3 might no longer fit into the predator's mouth (Truemper & Lauer, 2004). At the other end of the
4 spectrum prey can also become too small for a predator, approaching invisibility, an effect that
5 may result without necessarily invoking active selectivity when prey size falls under an assumed
6 detectability threshold. Therefore, the relationship displayed in Fig. 2 is expected to eventually
7 approach zero again to become curvilinear towards ever-larger predator/prey size ratios (to the
8 right: Vucic-Pestic *et al.*, 2010), as hinted by our non-linear fit (which however fitted no better
9 here, based on AIC). At this point the prey might no longer be interesting for or even detected by
10 many predators, ultimately resulting in no predation and hence no data, as occurred for some of
11 our tested amphibians (Table 1). Even though we initially tested several additional amphibian and
12 arthropod predators, we perhaps inevitably ended up with a less than optimal, seemingly
13 haphazard assortment of predator-prey pairings that behaved naturally (enough) in our
14 experimental laboratory setting. Nonetheless, we deem our study representative and useful in this
15 context.

16 In mixed-sex groups predation risk was not higher than in single sex groups (Figs. 1, 3),
17 generalizing similar earlier results for *Sc. stercoraria* preying upon *Se. cynipsea* (Mühlhäuser &
18 Blanckenhorn, 2002; Teuschl *et al.*, 2010). This was unexpected, as mating is a conspicuous
19 behavior that should attract predators and at the same time distract the prey. However, while we
20 observed some mating activity during our experiments, it was not quantified here, so we cannot
21 address this hypothesis rigorously. We also expected predation rates to vary according to prey
22 sex, if only because of size dimorphism, but this did not occur in general either, merely in the
23 particular cases of *Rana temporaria* juveniles preying on *Se. cynipsea*, and *Sc. stercoraria*

1 preying on *Se. thoracica* (Fig. 3). In this context, we expected the typically more mobile males to
2 be subject to more predation than females (Teuschl *et al.*, 2010), which also did not occur;
3 whereas *Rana temporaria* juveniles indeed took more male than female prey, this was not the
4 case for any other predator (Fig. 3). Admittedly, lack of demonstrable sex-specific predation may
5 relate to limitations of our experimental set-up. We nevertheless conclude, based on our limited
6 sample here, that sex differences in viability selection exerted by single predators appear to be
7 rare, and therefore likely contribute little to sexual dimorphism (cf. Blanckenhorn, 2000, 2005).

8 Surprisingly, the conspicuous orange coloration of large *Se. thoracica* males did not make
9 them more vulnerable to predation by *Sc. stercoraria*, which in fact ate more females than males,
10 perhaps because they are more sluggish and easier to catch (Fig. 3). Although many insect and
11 spider groups lack a visual receptor in the red part of the spectrum (Briscoe & Chittka, 2001;
12 Théry & Gomez, 2010; Fabricant & Herberstein, 2015), potentially making orange-colored prey
13 cryptic against a green grass background, this is not generally the case for amphibians (Fite,
14 1976). Our results suggest that, at least for the sit-and-wait predators tested here, movement
15 seems more important than coloration (Busso & Blanckenhorn, 2018a).

16 In conclusion, although haphazard in terms of predator/prey relationships and certainly
17 incomplete, our study of a guild of sit-and-wait amphibian and arthropod predators of insects
18 inhabiting a common temperate grassland landscape added valuable experimental evidence
19 elucidating the multiple factors influencing size-selective predation within species. We
20 nevertheless hope to have shown that, because each predator imposes a different selection
21 pressure on prey body size, from the prey perspective viability selection in the field must be
22 integrated across various predators to obtain net selection. In the end the overall predation
23 selection on a given prey species may well be zero. Conclusively demonstrating this

1 experimentally is difficult if not impossible, however, given the multifarious predator-prey
2 relationships in any ecosystem, many of them unspecific. Functional, trait-based investigations of
3 interactions between single predator and prey species, as conducted here, are a good start, but
4 necessarily remain incomplete. More comprehensive phenomenological studies of selection in the
5 wild, which unfortunately often do not consider predator species identity or investigate concrete
6 mechanisms, thus remain indispensable when taking the prey perspective (e.g. Blanckenhorn *et*
7 *al.*, 1999; Jann *et al.*, 2000).

8

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Table 1. Combinations of predators and prey used (X), with number of tested replicate prey groups (of females, males, mixed) in parentheses, and size ranges (snout vent length for amphibians; total length for arthropods). 0: attempted but too little predation; –: not attempted.

Predators		Prey			
Amphibians	n	<i>Sc. stercoraria</i>	<i>Se. cynipsea</i>	<i>Se. thoracica</i>	
<i>Bombina variegata</i>	11	X (10,10,28)	0	–	27 - 38
<i>Bufo bufo</i>	4	X (25,25,50)	X (14,15,30)	–	55 - 82
<i>Rana esculenta</i>	8	X (10,10,28)	0	–	58 - 74.5
<i>Rana temporaria</i> (juv.)	4	0	X (14,14,28)	–	13.6 - 14.7
<i>Rana ridibunda</i>	5	0	0	–	
<i>Triturus alpestris</i>	6	0	0	–	
<i>Salamandra salamandra</i>	3	0	0	–	
Arthropods					
<i>Heliophanus flavipes</i> *	49	0	–	X (0,44,0)	5.8 - 12.4
<i>Himacerus mirmicoides</i> *	52	0	–	X (0,45,0)	11.4 - 14.3
<i>Scathophaga stercoraria</i> §	32	–	X (10,10,20)	X (0,39,56)	6.3 - 10.6
*no female prey treatment		7.3 - 11.8	3.7 - 8.1	4.8 - 9.2	size range (mm)
§data from Teuschl et al. 2010					

Figure 1

Standardized mean viability (i.e. predation) selection differentials ($\pm 95\%$ CI) for various predators ((a-e) amphibian vertebrates; (f-i) arthropods) and treatments (all-male, all-female, mixed-sex) on various dung fly prey species. Male prey are represented as squares and female prey as circles. Overlapping 95% CI intervals with the zero line indicate no significant selection.

Figure 2

Overall mean standardized viability (i.e. predation) selection differential per predator/prey species combination (N=9) as a function of the average (total or snout-vent) body length ratio between the predator and the prey. The quadratic fit is no better than the linear fit, based on AIC.

Figure 3

Proportional differences in the numbers of males and females eaten in the mixed-sex treatments $((m-f)/(m+f))$ for all predator/prey species combinations. Overlapping 95% CI intervals with the zero line indicate no significant sex bias.

Photo credits:

1		
2		
3	<i>Scathophaga stercoraria</i>	Hayat Mahdjoub (ex Post-doc of our lab)
4	<i>Sepsis cynipsea</i>	Oliver Niehuis (collaborating colleague, Univ. of Freiburg, D)
5	<i>Sepsis thoracica</i>	Juan Pablo Busso (ex PhD student of our lab)
6	<i>Bufo bufo</i>	Josh van Buskirk (local colleague)
7	<i>Rana esculenta</i>	https://www.istockphoto.com/it/immagine/rana-esculenta
8	<i>Rana temporaria</i>	Christoph Vorburger (local colleague)
9	<i>Bombina variegata</i>	https://www.tumblr.com/search/bombina+variegata
10	<i>Heliophanus flavipes</i>	
11		https://arthropodafotos.de/dbsp.php?lang=deu&sc=0&ta=t_2_ara_lab_sal&sci=heliophanus&scisp=flavipes
12	<i>Himacerus mirmicoides</i>	http://www.britishbugs.org.uk/heteroptera/Nabidae/himacerus_mirmicoides.html