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RESEARCH ARTICLE

Quantifying predator functional responses under field conditions reveals interactive effects of temperature and interference with sex and stage

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Abstract

1. Predator functional responses describe predator feeding rates and are central to predator–prey theory. Originally defined as the relationship between predator feeding rates and prey densities, it is now well known that functional responses are shaped by a multitude of factors. However, much of our knowledge about how these factors influence functional responses is based on laboratory studies that are generally logistically constrained to examining only a few factors simultaneously and that have unclear links to the conditions organisms experience in the field.
2. We apply an observational approach for measuring functional responses to understand how sex/stage differences, temperature and predator densities interact to influence the functional response of zebra jumping spiders on midges under natural conditions.
3. We used field surveys of jumping spiders to infer their feeding rates and examine the relationships between feeding rates, sex/stage, midge density, predator density and temperature using generalized additive models. We then used the relationships supported by the models to fit parametric functional responses to the data.
4. We find that feeding rates of zebra jumping spiders follow some expectations from previous laboratory studies such as increasing feeding rates with body size and decreasing feeding rates with predator densities. However, in contrast to previous results, our results also show a lack of temperature response in spider feeding rates and differential decreases in the feeding rates of females and juveniles with densities of different spider sexes/stages.
5. Our results illustrate the multidimensional nature of functional responses in natural settings and reveal how factors influencing functional responses can interact with one another through behaviour and morphology. Further studies investigating the influence of multiple mechanisms on predator functional

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responses under field conditions will increase our understanding of the drivers of predator–prey interaction strengths and their consequences for communities and ecosystems.

KEYWORDS

feeding rates, foraging, intraspecific variation, jumping spiders, predator–prey interactions, sexual dimorphism

1 | INTRODUCTION

Functional responses describe predator feeding rates and are central to understanding predator–prey interactions and the structure of food webs. Functional responses were originally defined as the relationship between predator feeding rates and prey densities (Holling, 1959; Solomon, 1949). In the intervening decades, we have discovered a multitude of factors other than resource densities that influence predator feeding rates such as: predator density/interference (DeLong & Vasseur, 2011; Hassell & Varley, 1969; Novak & Stouffer, 2021), temperature (Thompson, 1978; Uiterwaal & DeLong, 2020), predator and prey body sizes (Rall et al., 2012; Uiterwaal & DeLong, 2020; Vucic-Pestic, Rall, et al., 2010) and habitat complexity (Mocq et al., 2021; Toscano & Griffen, 2013). We also have learned that the effects of these factors on predator feeding rates have important ramifications for population dynamics (Beddington, 1975; Coblenz & DeLong, 2020; Murdoch & Oaten, 1975) and are critical for understanding how changes in climate, habitat and the movement of species influence predator–prey interactions and communities (Dick et al., 2014; Gilbert et al., 2014; Mocq et al., 2021).

Although we know that a variety of factors shape functional responses, we know less about how these factors interact (DeLong, 2021). One reason is that nearly all predator functional responses have been measured under laboratory conditions (Uiterwaal et al., 2018). This creates two issues. First, generally only one factor can be crossed with prey density because adding factors greatly increases the sample size and number of organisms required. Second, it is often unclear how relevant laboratory treatments and conditions are to the conditions that organisms experience naturally (Griffen, 2021). For example, studies on how temperature influences functional responses rarely mention whether the temperature range used corresponds to the temperatures experienced by species in the field. Together, these two issues hinder our understanding of how multiple factors interact to shape functional responses and diminish the relevance of laboratory experiments to our understanding of natural populations.

A promising complement to laboratory functional response experiments are observational approaches (Beardsell et al., 2021; Novak et al., 2017; Novak & Wootton, 2008; Preston et al., 2018). Observational approaches allow functional responses to be measured under natural conditions. Using natural variation in ecological conditions, one simultaneously can assess the effect of multiple factors on functional responses while guaranteeing that the range of variation is relevant to those experienced by the organisms in the field.

Here we use an observational approach to examine how temperature, predator interference and sex/stage influence the functional response of zebra jumping spiders (*Salticus scenicus*) foraging on midges (*Chironomidae* spp.). Zebra jumping spiders provide a useful study system because: (a) many laboratory functional response experiments have been performed on arthropod predators feeding on arthropod prey, facilitating comparisons between the observational approach and laboratory studies (Uiterwaal et al., 2018) and (b) zebra jumping spiders are easily observable foraging and thus amenable to observational approaches. We focus on sex/stage, temperature and interference because these factors are well-known to influence predator functional responses in laboratory studies, yet their simultaneous effects on feeding rates in field conditions are unknown.

Sex/stage in zebra jumping spiders is likely to influence feeding rates through two mechanisms: (a) size differences among the sexes/stages and (b) differences among sexes in morphology and behaviour. In zebra jumping spiders, adult females are largest, followed by adult males, and juveniles are the smallest (male and female juveniles cannot be distinguished by casual observation; Figure 1). Predator body size is well-known to influence predator functional responses (Rall et al., 2012; Uiterwaal & DeLong, 2020; Vucic-Pestic, Rall, et al., 2010), and, based on these previous results, females would be expected to have the highest space clearance rates (a.k.a. attack rates) and lowest handling times, and juveniles would be expected to have the lowest space clearance rates and highest handling times given similar sized prey. However, body size is not the only difference between sexes/stages in zebra jumping spiders. Zebra jumping spiders exhibit sexual dimorphism as adults, with males having enlarged chelicerae and an overall darker colour (Figure 1a,b). Furthermore, male spiders of many species often exhibit no or weak functional responses due to differences in sexual roles among females and males (Givens, 1978; Walker & Rypstra, 2002). Thus, we hypothesized that females would exhibit greater feeding rates than males and juveniles, while the relative differences between juveniles and males would depend on the extent to which males foraged and whether the enlarged chelicerae impeded foraging.

Laboratory studies generally show that temperature alters the functional responses of ectotherms (DeLong, 2021; Englund et al., 2011; Rall et al., 2012; Uiterwaal & DeLong, 2020; West & Post, 2016). In line with physiological expectations, space clearance rates typically increase or have a unimodal, concave relationship with temperature whereas handling times typically decrease or have a unimodal, convex relationship with temperature (Burnside et al., 2014; DeLong & Lyon, 2020; Englund et al., 2011; Rall et al., 2012). It remains



FIGURE 1 Female (a), male (b), and juvenile (c) zebra jumping spiders. The light grey grids on the grid paper are 2 mm

unclear, however, how these temperature effects translate to field conditions. Laboratory experiments examining the effects of temperature typically occur in simplified arenas in which predators and prey are exposed to a constant temperature for the length of the feeding trial (e.g. Archer et al., 2019; Broom et al., 2021). This experimental design isolates the effects of temperature but prevents organisms from behaviourally thermoregulating by, for example, using thermal refugia as they might in the field (May, 1979). If predators behaviourally thermoregulate while foraging in field contexts, then the effects of temperature on functional responses may be dampened. Predators also may take advantage of diurnal changes in temperature and forage only when temperatures are suitable (May, 1979), which also could dampen temperature effects. Therefore, we hypothesize that, under field conditions, the effects of temperature on feeding rates are likely to be less pronounced than expected from laboratory-based results.

Functional responses generally decrease with the densities of predators (DeLong & Vasseur, 2011; Novak & Stouffer, 2021). However, most of the studies that demonstrate this effect have taken place in simplified, enclosed arenas. It is unclear how behaviour in response to the presence of other individuals in such arenas might translate to field conditions. Furthermore, studies on the effects of predator densities generally only consider the effects of similar individuals, even though interference between predators can be stronger, for example, between adults and juveniles than between juveniles and juveniles (Sih, 1981). How interference operates when individuals are exposed to multiple predator types simultaneously is unknown. For zebra jumping spiders, we hypothesized that predator densities would reduce feeding rates for each sex/stage and that the effects of adult densities would be stronger on juveniles than vice versa.

2 | MATERIALS AND METHODS

2.1 | Study system

Zebra jumping spiders have a Holarctic distribution and are common on artificial structures. At our field site at Cedar Point Biological Station, Ogallala, Nebraska, USA (41.2 N, 101.6 W), zebra jumping spiders are common on the outer walls of buildings. The spiders

forage on a variety of invertebrate prey (Okuyama, 2007), but most of their diet in the summer on these walls consisted of midges despite the availability of alternative prey (see Results). We therefore focused on jumping spiders foraging on midges. These spiders are well-suited for the use of observational approaches as they are readily observable feeding on their prey and the times for which the feeding events are detectable are readily measurable (see Detection Time Surveys below).

2.2 | Observational approach to measuring functional responses

We first introduce how observational data can be used to estimate feeding rates. We then describe the methods used to collect the required data and the statistical methods used to examine spider feeding rates and fit functional response models.

The observational approach to estimating functional responses we use relies on the fact that a predator's feeding rate together with the time over which interactions are detectable gives the expected proportion of time that individuals are observable feeding (Novak et al., 2017; Novak & Wootton, 2008). For a predator with feeding rate, f , the number of prey eaten by that predator over time, T , is fT . If d is the time that the interaction is detectable (i.e. the time predators spend eating a single prey—not to be confused with the time it takes a predator to detect an individual prey item), the total time a predator is observable feeding is fdT and the proportion of time a predator is observable feeding is fd . Assuming individuals have the same feeding rate, then, in a snapshot survey across individuals, the proportion of individuals feeding, p , should also be fd , and the feeding rate of the predators therefore can be estimated as $f = \frac{p}{d}$.

To estimate feeding rates and the factors influencing the functional response, we need several pieces of information. First, from observational surveys, we need the number of predators feeding and not feeding and any associated information to be used in the functional response such as prey/predator densities and temperature. We also need an estimate of the detection time d or how long, on average, the predators are observable feeding on a prey item. Below, we first describe how we performed our feeding surveys. We then describe how we estimated the detection times of zebra jumping

spiders on midges. Last, we describe the statistical methods we used to combine these data and estimate the functional response.

2.3 | Feeding surveys

Between 29 May 2020 and 14 June 2020, during the breeding season of the spiders, we performed 155 snapshot feeding surveys across 17 building-wall combinations at Cedar Point Biological Station (building-wall combinations refers to separate walls on buildings being separate sampling units). We performed surveys between 830 and 1600, as spiders generally were not foraging outside of this time range. We surveyed specific building-wall combinations at most three times per day. We treated surveys as independent because the time between successive surveys was longer than the detection times of predators feeding on prey.

Before each survey, we measured the temperature at 4 to 12 spots along the wall using an infrared thermometer (Raytek Raynger ST, Fluke Corporation). Afterwards, we systematically moved from one end of the wall to the other searching vertically to a standardized height of 1.75 m. As we moved along the wall, we gave each observed spider a unique ID. We wrote this ID on a piece of paper with either a 2 or 6.35 mm grid. We recorded the spider's sex/stage, whether the spider was feeding, what the spider was feeding on, and, if the spider was feeding on a midge, a description of its size [categorized as small ($\sim \leq 5$ mm), medium ($\sim 5 - 10$ mm), or large ($\sim \geq 10$ mm)]. We then photographed the spider with the grid paper visible in the photograph. We also recorded each midge we observed on the wall and classified them into the same size categories as for the midges being consumed. From these data, we derived the number of spiders of each sex/stage feeding and not feeding on midges, the total number of midges, and a mean temperature across the wall.

After the surveys, we measured the lengths of spiders from the photographs using ImageJ (Schneider et al., 2012). We were unable to get sizes for every individual because some spiders hid or leapt from the wall before being photographed, some photographs were not of high enough quality, and two surveys were missing photographs. For these spiders [47 of 644 females (7.3%), 41 of 286 males (14.3%) and 13 of 172 juveniles (7.6%)], we estimated their size as the mean size for that sex/stage across the experiment. Although the proportions of missing photographs differed among sexes/stages (chi-square test, $\chi^2 = 12.4$, $df = 2$, $p = 0.002$; Supplementary Material 1, Figure S1), the similar proportions of missing photographs for females and juveniles suggests that the differences in missing photographs were not associated with size, and therefore mean imputation of missing values is unlikely to influence our results.

2.4 | Detection time estimates

To use the observational approach, one needs an estimate of how long predator feeding events are observable (i.e. detection times).

To estimate detection times, we fed midges to spiders and recorded the length of time from when the spider attacked the midge until the spider subsequently dropped the midge. We made these measurements between 29 May 2020 and 13 June 2020 and between 15 June 2021 and 18 June 2021. We performed additional trials in 2021 because the detection time trials in 2020 did not cover the full temperature range of the 2020 feeding surveys. To conduct a trial, we captured midges in clear plastic vials and placed the vial opening over a spider on a wall until the spider attacked the midge. Spiders were generally returned to the wall after attacking the midge, but, in cases in which the spider refused to return to the wall, they were left to feed inside the vial placed near the wall. We then recorded the attack time, the temperature using an infrared thermometer, and the time the spider dropped the midge. During the feeding surveys, we also occasionally observed a spider as it caught a midge. When this was the case, we recorded the time, temperature and the time at which the spider dropped the midge. For all detection time observations, we also took photographs of the spider with grid paper containing a unique ID from which we later measured the spider length in ImageJ.

From these data, we estimated the effects of midge size, predator size and temperature on detection times using multiple linear regression through the `BRMS` package (Bürkner, 2017) in R (v. 4.0.5; R Core Team, 2020). We log transformed the detection times, spider length and temperature to meet model assumptions. We used default priors with four Hamiltonian Monte Carlo chains with 1000 sampling iterations and a warm-up of 1,000 iterations. We did not include sex/stage in the model as including sex/stage reduced the predictive ability of the model according to the widely applicable information criterion (WAIC, a Bayesian information criterion analogous to AIC, Watanabe, 2013). Therefore, the regression model and our estimates of detection times for surveys below include no additional effect of sex/stage on detection times beyond differences in body sizes.

Using the model fit to the detection time survey data, we estimated an average detection time of zebra jumping spiders feeding on midges for females, males and juveniles in each survey for which they were present. Partway through the feeding surveys, we standardized observers' definitions of midge size. For each survey, we first determined observer-corrected midge densities of each size for surveys before 6 June 2020. On this date, the observers met and standardized definitions for small, medium and large midges. Correction factors for each observer were calculated by determining the differences in the number of small, medium and large midges in surveys post-June 6 between each observer's pre-June 6 definitions of prey sizes and post-June 6 definitions. We also used differences in prey sizes from the reclassification of prey sizes from photographs of feeding spiders pre-June 6. The differences in proportions of midges in each size class pre- and post-June 6 were used to correct the pre-June 6 number of midges in each size class for each observer. We then calculated the mean spider length in each survey for each sex/stage and used the regression model to calculate a mean detection time.

2.5 | Estimating functional responses

To examine the effects of temperature, sex/stage and predator densities on the jumping spider functional response, we performed a two-stage analysis. We first estimated predator feeding rates using the proportions of predators feeding in each survey and the measured detection times. We then used hierarchical generalized additive models (GAMs) to examine the relationships between feeding rates, temperature and predator densities. After using model comparison to determine relative support across a suite of models, we fit parametric functional response models representing the functional response forms suggested by the GAMs. We chose this route of analysis for two reasons. First, functional responses can take a variety of shapes. As GAMs fit smooth functions of covariates to the data, we could infer which functional response shapes were appropriate for the parametric functional response analysis. Second, the parametric functional response analysis provides estimates of biologically interpretable parameters and their uncertainty.

2.6 | GAM feeding rate analysis

Using the feeding rates estimated for each survey, we fit a suite of hierarchical GAMs for each sex/stage. We considered seven different models for the feeding rates of each sex/stage: (a) a full model with midge density, the densities of each sex/stage separately and temperature, (b) a model with midge density, the combined densities of spiders across sex/stage and temperature, (c) a model with midge density and temperature, (d) a model with midge density and the densities of each sex/stage separately, (e) a model with midge density and the combined densities of spiders across sex/stage, (f) a model with midge density only and (g) an intercept-only model. To account for the non-independence of surveys on the same building-wall combination, we included building-wall combination as a random effect. We also weighted each observation by its sample size (total number of spiders in the survey) relative to the mean sample size to account for differences in confidence of the feeding rate estimates. We used an identity link with the feeding rates as the response variable. For each model, we examined estimates of concurvity (analogous to multicollinearity in multiple regression) to ensure that our results were robust. After fitting the models, we used AIC (Akaike, 1974) to determine relative support for the models. We fit the GAMs using the `MCMC` package (Wood, 2017) in R (v. 4.0.5; R Core Team, 2020).

2.7 | Parametric functional response fitting

To fit parametric functional response models to the data, we again use the link between the feeding rates of a predator and the proportion of predators observed feeding. With one prey species, predators are either feeding or not feeding (spiders not feeding on midges were considered not feeding). In this case, we can model the proportion of feeding events as following a binomial distribution. Using

the surveys of the number of feeding and not feeding spiders across midge densities, temperature and predator densities, we can model the number of individuals feeding in each survey i , y_i , as

$$y_i \sim \text{Binomial}(p_i = f_i d_i n_i), \quad (1)$$

where p_i is the estimated proportion of individuals in survey i feeding, f_i is the estimated feeding rate of predators in survey i , d_i is the detection time for survey i and n_i is the total number of predators in survey i . After substituting the functional response suggested by the GAM models for f_i , we estimated the parameters of that functional response using Bayesian inference.

For females, the GAM analysis suggested a saturating (type II) functional response model with a decline in feeding rates associated with the total densities of predators. We therefore assumed a Beddington–DeAngelis model for the functional response

$$f_i = \frac{aR_i}{1 + ah_iR_i + \gamma C_i}, \quad (2)$$

where a is the predator space clearance rate, R_i is the density of midges in survey i , h_i is the predator handling time in survey i , γ is the predator interference (time wasted) and C_i is the combined predator density in survey i .

For juveniles, the GAM analysis suggested a functional response model with a saturating or unimodal, concave relationship with midge densities, separate effects of each sex/stage density on feeding rates, and a potentially decreasing effect of temperature. We therefore fit two functional response models to the juvenile data: (a) a Beddington–DeAngelis type model with a temperature-dependent space clearance rate, and (b) a Beddington–DeAngelis type model with a temperature-dependent space clearance rate and a unimodal relationship between feeding rates and midge densities (a Type IV or dome shape). We modelled temperature dependence of the space clearance rate assuming that the space clearance rate had an exponential relationship with temperature that could be quadratic:

$$a_i(T_i) = c_a e^{b_a T_i + q_a T_i^2}, \quad (3)$$

where a_i is the space clearance rate of the predators in survey i at temperature T_i , and c_a , b_a , and q_a are parameters describing the relationship between space clearance rates and temperature across surveys. The Beddington–DeAngelis type model with a temperature-dependent space clearance rate we used was

$$f_i = \frac{a_i(T_i)R_i}{1 + a_i(T_i)h_iR_i + \gamma_J J_i + \gamma_F F_i + \gamma_M M_i}, \quad (4)$$

where γ_J , γ_F and γ_M are the interference rates associated with juvenile, female and male densities J_i , F_i and M_i respectively. To model a unimodal relationship between midge densities and the feeding rate we used a model combining a Beddington–DeAngelis-like model with a Type IV model from Fujii et al. (1986),

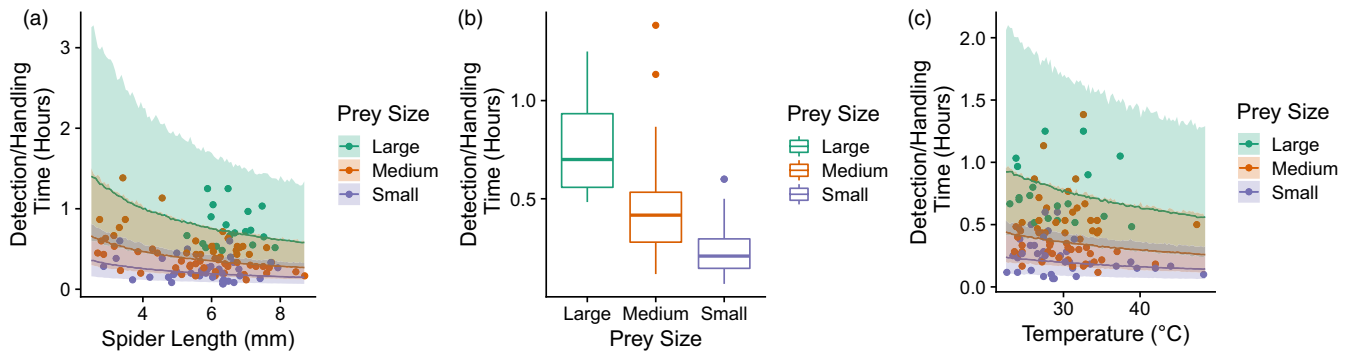


FIGURE 2 Zebra jumping spider detection/handling times decreased with increasing spider length (a), decreasing prey (midge) size (b), and increasing temperature (c). Lines in a and c are calculated with average temperature and spider length across the detection time experiment, respectively. The ribbons around the lines in a and c are 90% prediction intervals

$$f_i = \frac{a_i(T_i)R_i e^{wR_i}}{1 + a_i(T_i)h_i R_i e^{wR_i} + \gamma_J J_i + \gamma_F F_i + \gamma_M M_i}, \quad (5)$$

where all parameters are defined above except for w which leads to a concave relationship between feeding rates and prey densities when negative.

For males, the data strongly violated the assumptions of GAMs due to a large proportion of surveys with feeding rates that were zero (see Results). Therefore, we did not fit a parametric functional response to the male data.

We fit each of the functional response models in a Bayesian framework using the program Stan through R using the package RSTAN (Stan Development Team, 2021). As a simplifying assumption, we assumed that the handling times for each survey were equivalent to the detection times (i.e. $h_i = d_i$). Although doing so assumes that the handling times are equivalent to the time consuming prey items and excludes the portion of digestion that occurs after dropping the prey, we believe this assumption is valid for the actively foraging spiders on the walls we observed. Note that these handling times incorporate the effects of average spider body size, temperature and the sizes of prey available for each survey. We used weakly informative or regularizing priors on each of the parameters. For c_a and the temperature-independent space clearance rate a , we used a Normal(mean = 10, standard deviation = 15) prior truncated at zero derived from invertebrate predators feeding on invertebrate prey in the FoRAGE (Functional Responses Around the Globe in all Ecosystems) database (Uiterwaal et al., 2018). For b_a and q_a and the interference parameters, we used Normal(mean = 0, standard deviation = 1) priors.

All data and code associated with the analyses are available (see Data Availability Statement). Our research was conducted in an ethical manner but did not require ethical approval.

3 | RESULTS

Out of 155 surveys, we observed females in 147 surveys, males in 112 surveys and juveniles in 96 surveys. These surveys contained 644 observations of females (mean of 4.3 per survey, mean spider

length 6.5 mm), 286 observations of males (mean of 2.5 per survey, mean spider length 5.0 mm) and 172 observations of juveniles (mean of 1.8 per survey, mean spider length 3.8 mm). For females, 41% of the observations were feeding observations of which 92% were on midges, for males, 14% of the observations were feeding observations of which 96% were on midges, and for juveniles, 24% of the observations were feeding observations of which 97% were on midges. The mean wall temperatures ranged from 15.7°C to 44.7°C.

3.1 | Detection/handling times

In total, we made 82 detection time observations on females, 18 observations on males and 17 observations on juveniles. Detection/handling times decreased with increasing spider length and temperature and decreasing prey size (Figure 2). We estimate that a 10% increase in spider length reduces detection/handling times by 6.8% [90% credible interval (CrI) 4.2–9.3%] and a 10% increase in temperature reduces detection/handling times by 6.4% (90% CrI 2.1–10.9%; Figure 2a,c). Feeding on a medium sized midge reduces the geometric mean detection/handling time by 53% (90% CrI 42.9–62%) relative to large midges and feeding on small midges reduces the geometric mean of the detection/handling time by 74.6% (90% CrI 68.3–79.4%) relative to large midges (Figure 2b).

3.2 | Feeding rate-covariate relationships

Model selection for GAMs revealed different suites of covariates in the top performing models for females and juveniles (Table 1). We were unable to perform model selection on the male models because the large proportion of surveys with no male spiders feeding prevented the data from meeting model assumptions (19 of the 112 surveys had males feeding; Figure 3c). For females, the top performing model included midge density and the combined densities of all predator age/sex stages (Table 1). Female feeding rates showed an increasing, saturating relationship with midge densities and a decreasing relationship with total predator densities (Figure 3a,b). For juveniles, the top performing models included midge density,

TABLE 1 AIC values for the generalized additive models (GAMs) fits for female and juvenile zebra jumping spider feeding rates as a function of suite of potential covariates. Δ AIC gives the differences between the lowest AIC value and the AIC value for each model, and model weights calculated give the relative likelihoods of each model

Model	AIC	Δ AIC	Model weight
Females			
No Temp.	301.42	0	0.53
Interference combined			
+Temp. Interference combined	303.3	1.88	0.21
No Temp.	305.28	3.86	0.08
Interference separate			
No Temp. No Interference	305.47	4.05	0.07
+Temp. Interference separate	305.72	4.3	0.06
+Temp. No interference	306.01	4.59	0.05
Null	376.08	74.66	0
Juveniles			
+Temp.	220.95	0	0.47
Interference separate			
No Temp. Interference separate	220.97	0.02	0.46
No Temp. Interference combined	227.06	6.12	0.02
No Temp. No interference	227.08	6.14	0.02
+Temp. No interference	227.53	6.59	0.02
+Temp. Interference combined	228.48	7.54	0.01
Null	235.97	15.03	0

separate densities of each predator stage/sex and temperature and the same model with no temperature (Table 1). Juvenile feeding rates showed an increasing saturating or concave, unimodal relationship with midge densities, a statistically unclear relationship with juvenile and male densities, a decreasing relationship with female densities, and a statistically unclear relationship with temperature (Figure 3d–3h).

3.3 | Parametric functional response fits

The parametric functional response fit for females estimated a space clearance rate of 3.37 m²/hour [90% credible interval (CrI) 2.48–4.59] and an interference parameter of 0.98 (90% CrI 0.23–1.93; Figure 4). The parametric functional response fit for juveniles with an increasing, saturating relationship between feeding rates and midge densities estimated a weak but possibly unimodal convex relationship between space clearance rates and temperature ($c_a = 16.4$, 90% CrI 3.1–37.6; $b_a = -0.2$, 90% CrI -0.3 to -0.08; $q_a = 0.004$, 90% CrI 0.001–0.005). The model also estimated the interference associated with juvenile densities as -0.5 (90% CrI -2.0–1.2), the interference associated with females as 1.0 (90% CrI 0–2.3) and the interference associated with males as 0.3 (90% CrI -1.1–1.7; Figure 5). The parametric functional response fit for juveniles with a unimodal, concave relationship between feeding rates and midge densities also suggested a weak but possibly convex relationship between temperature and space clearance rates ($c_a = 17.1$, 90% CrI 3.2–37.3; $b_a = -0.1$, 90% CrI -0.2 to -0.02; $q_a = 0.002$, 90% CrI 0.0001–0.004).

The model also estimated the interference associated with juvenile densities as -0.6 (90% CrI -2.2–1.1), the interference associated with females as 1.2 (90% CrI 0.1–2.4), the interference associated with males as 0.1 (90% CrI -1.3–1.6), and the parameter controlling the convexity of the relationship between feeding rates and midge densities as -0.4 (90% CrI -0.6 to -0.2 (Figure 6).

4 | DISCUSSION

Using a field observational approach, we examined how sex/stage, temperature and predator densities influenced the feeding rates of zebra jumping spiders. Our results align with previous expectations for the effects of body size, differences among sexes in feeding rates and reduced feeding rates with higher predator densities. Yet, we found little evidence of an effect of temperature on feeding rates and found that sexes/stages cause similar reductions of female feeding rates but juveniles primarily respond to female densities. Therefore, our results suggest that feeding rates may respond differently to ecological conditions in the field than in the laboratory and illustrate how observational methods can simultaneously examine the effects of multiple variables on predator feeding rates.

Our results support the conclusion that both body size and behavioural differences shape feeding rate differences among sexes/stages. As expected from previous results on body sizes and functional responses, the larger-sized females showed higher feeding rates than juveniles (Rall et al., 2012; Uiterwaal & DeLong, 2020;

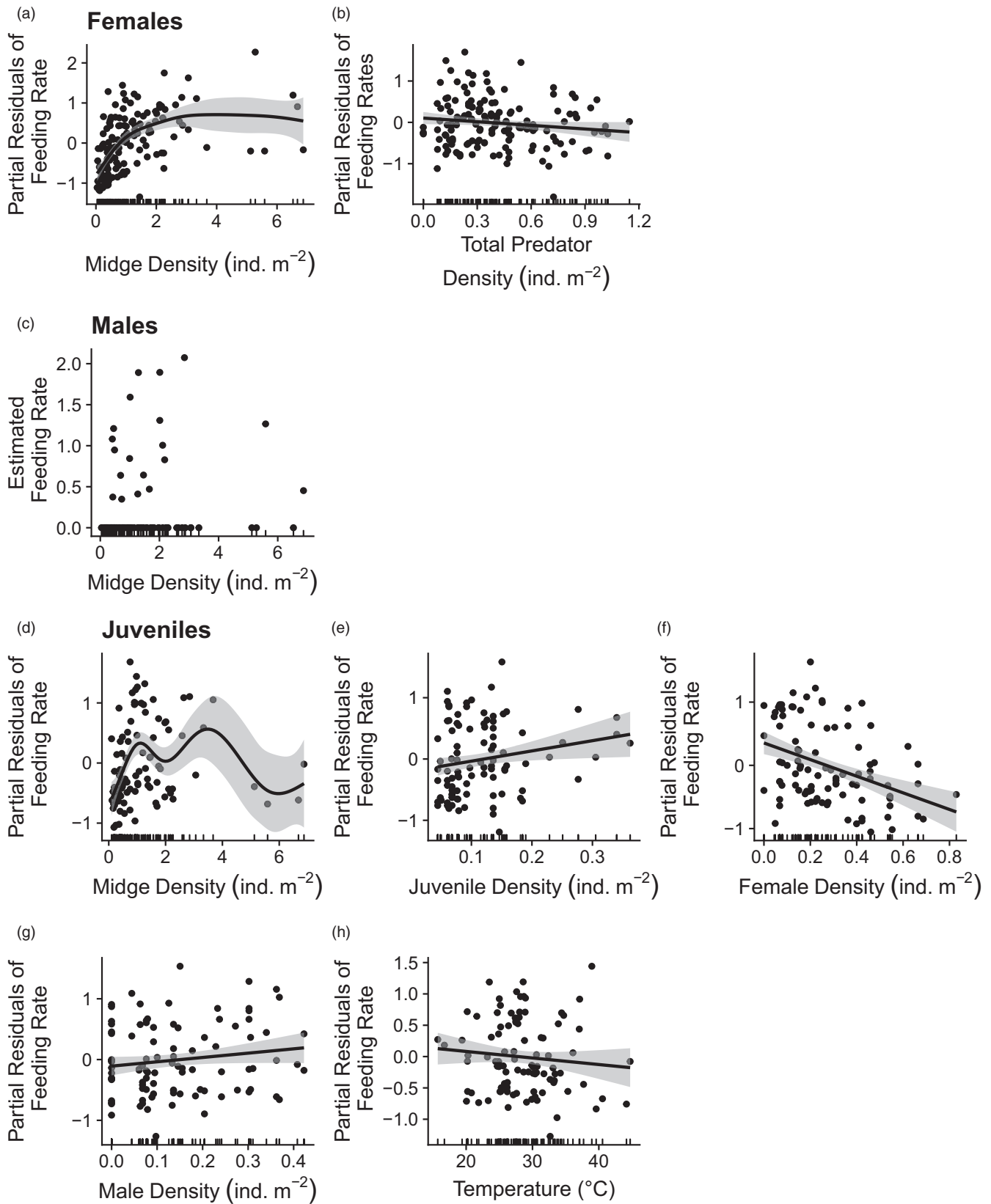


FIGURE 3 Generalized additive models (GAMs) with the lowest AIC scores predict different factors influencing female and juvenile feeding rates. GAMs were unable to be fit to male feeding rates as model assumptions could not be met. Panels a–b and d–h show the relationships between the residual feeding rates of the GAM models and the independent variables included in the models with the lowest AIC scores for females and juveniles, respectively. In each panel, the black lines represent the GAM fit for the mean relationship between the variable and the residual feeding rates and the shaded areas represent 90% confidence intervals on those relationships. In panel c, the y-axis is the raw estimated feeding rate

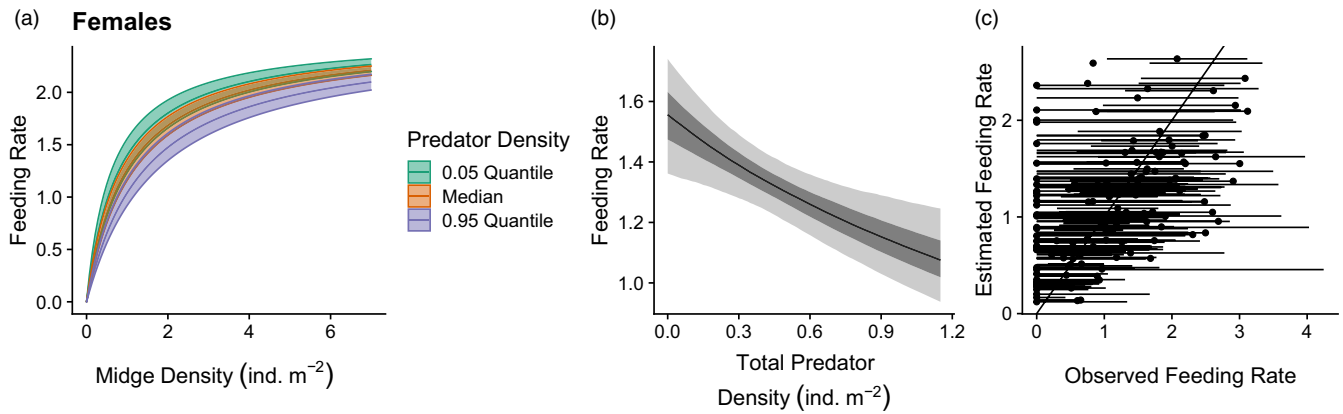


FIGURE 4 Parametric functional response predictions of female feeding rates with midge densities at different quantiles of total predator densities across surveys (a) and total predator densities (b). Lines in a and b represent predicted median feeding rates with all other variables at their across-survey means. Ribbons in a represent 90% credible intervals. The lighter and darker ribbons in b represent 90% and 50% credible intervals respectively. Panel c shows model-predicted and observed feeding rates. The diagonal line is the 1:1 line and the horizontal lines are the model 90% prediction intervals which give the interval in which 90% of future observations given the same covariates for each observation would be expected to fall

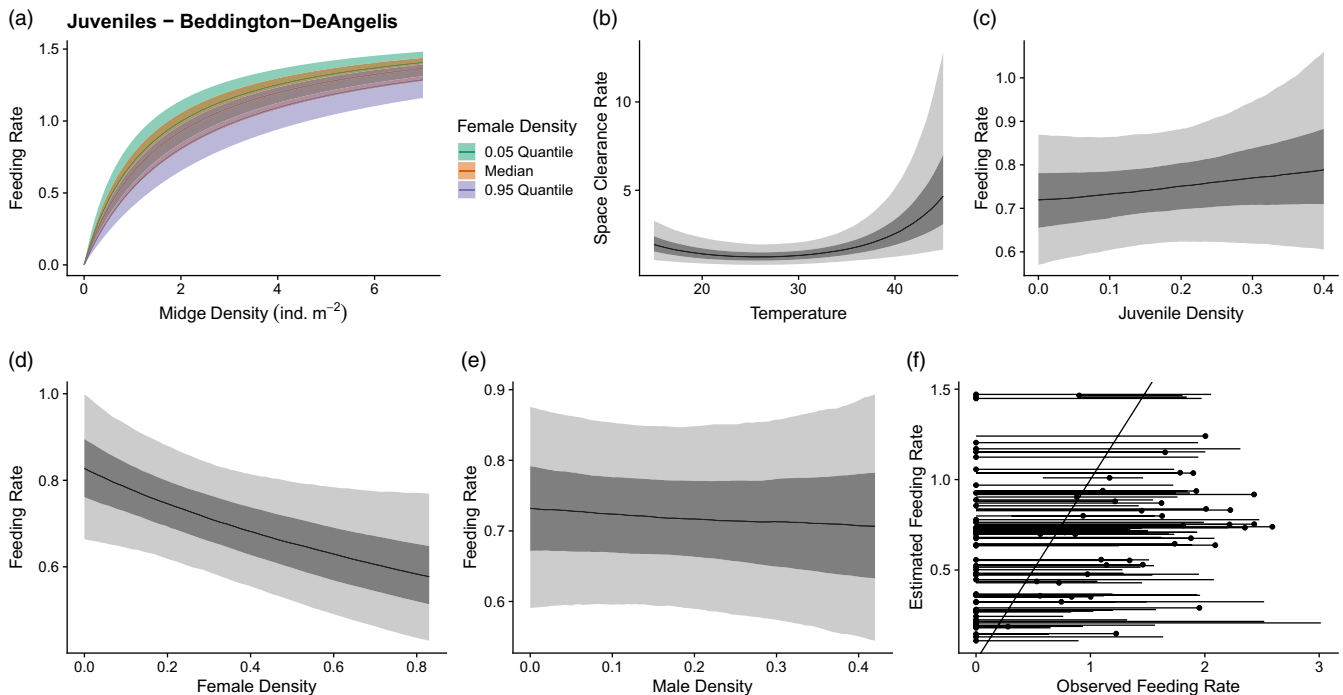


FIGURE 5 Parametric functional response predictions of juvenile feeding rate relationships with midge densities at different quantiles of female densities (a), juvenile densities (c), female densities (d) and male densities (e), and space clearance rate relationships with temperature (b) for the Type II Beddington–DeAngelis functional response. Lines in a–e represent predicted median feeding rates with all other variables at their across-survey means. Ribbons in A represent 90% credible intervals. The lighter and darker ribbons in b–e represent 90% and 50% credible intervals respectively. Panel f shows model-predicted and observed feeding rates. The diagonal line is the 1:1 line and the horizontal lines are the model 90% prediction intervals which give the interval in which 90% of future observations given the same covariates for each observation would be expected to fall

Vucic-Pestic, Rall, et al., 2010). Predator detection/handling times decreased with increasing spider size and increased with midge size, also as expected from previous results (Rall et al., 2012; Uiterwaal & DeLong, 2020; Vucic-Pestic, Rall, et al., 2010). However, space clearance rates did not differ appreciably in magnitude between females and juveniles. Together, these results suggest that the differences in

feeding rates between females and juveniles are largely due to their differences in handling times rather than space clearance rates. These results are in line with the findings of Uiterwaal and DeLong (2020) who showed that handling times declined with consumer body size more than space clearance rates increased with consumer body size across over 2,000 laboratory functional response experiments.

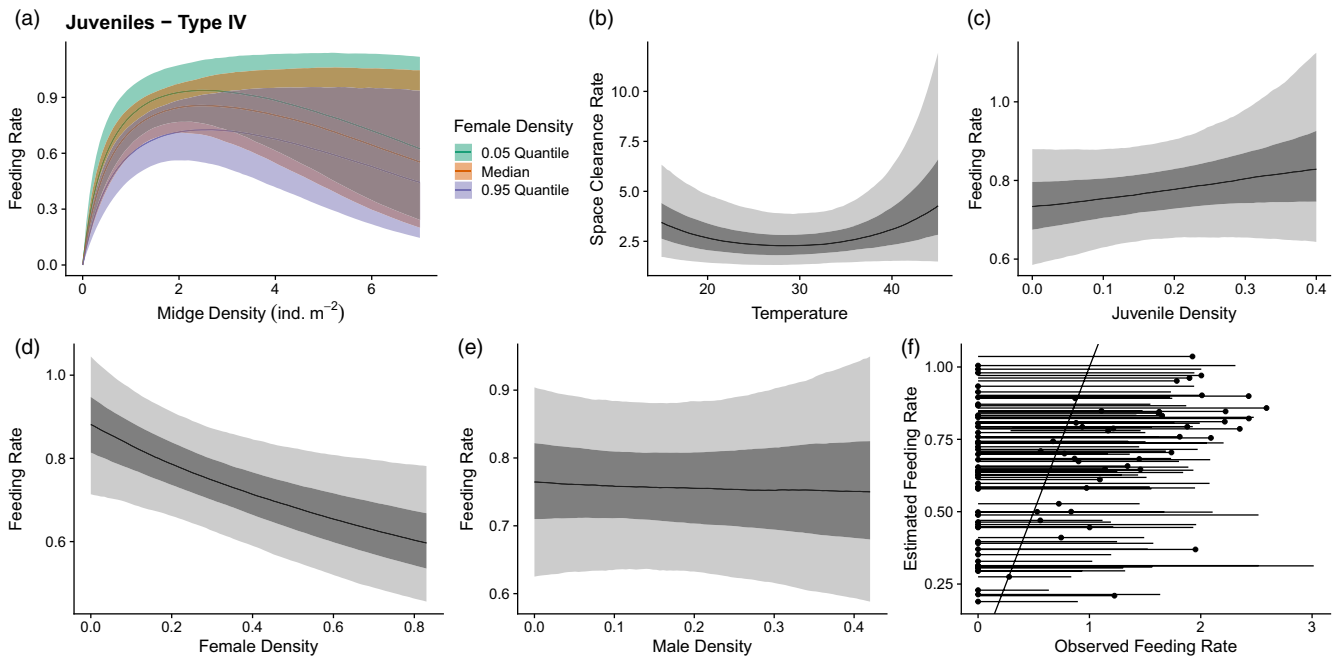


FIGURE 6 Parametric functional response predictions of juvenile feeding rate relationships with midge densities at different quantiles of female densities (a), juvenile densities (c), female densities (d) and male densities (e), and space clearance rate relationships with temperature (b) for the Type IV Beddington–DeAngelis functional response. Lines in A–E represent predicted median feeding rates with all other variables at their across-survey means. Ribbons in A represent 90% credible intervals. The lighter and darker ribbons in b–e represent 90% and 50% credible intervals respectively. Panel F shows model-predicted and observed feeding rates. The diagonal line is the 1:1 line and the horizontal lines are the model 90% prediction intervals which give the interval in which 90% of future observations given the same covariates for each observation would be expected to fall

Given that females and juveniles are not drastically different in body sizes, this appears to be a likely explanation for the lack of difference between females and juveniles in space clearance rates.

We found evidence of differences in functional response ‘type’ among the sexes and stages. Females exhibited a traditional saturating functional response (Type II), while juveniles showed some evidence of a Type IV or ‘dome-shaped’ functional response, and males did not exhibit a traditional functional response due to their minimal foraging activity. Previous studies on Type IV functional responses have attributed decreases in feeding rates at high prey densities to predator confusion, prey that are dangerous, exhibit group defences, or are nutritionally imbalanced for the predator, or habitat structure (Bressendorff & Toft, 2011; Jeschke & Tollrian, 2005; Líznavá & Pekár, 2013; Vucic-Pestic, Birkhofer, et al., 2010). Predator confusion or differences in nutritional requirements among females and juveniles could potentially play a role in this system, but group defences or effects of habitat structure seem unlikely. Furthermore, females could also exhibit a type IV functional response, but midge densities never reached a high enough density in the study for a decrease in feeding rates to appear. The type IV possibility, however, hinges on four observations of juvenile feeding rates at high midge densities (a parametric Type IV function response without these four observations estimates a w parameter of -0.03 90% CrI -0.4 – 0.35 , suggesting no evidence of a Type IV functional response; Supplemental Material 2). Follow-up studies could provide more definitive evidence of a Type IV functional response and elucidate the

underlying mechanism. We did not fit a functional response to male feeding rates as a majority of the male surveys had no spiders feeding. A lack of traditional functional response in males has also been seen in other spiders due to differences among sexes in reproductive roles (Givens, 1978; Walker & Rypstra, 2002). Females are likely to forage to maximize energy intake for the development of eggs, while males feed to meet a minimum energy requirement and devote more time to search for mating opportunities (Givens, 1978). Therefore, differences in the fitness benefits of foraging among sexes also likely shape differences in functional responses in this system.

Temperature is widely thought to play an important role in determining predator feeding rates by altering predator space clearance rates and handling times in ectotherms (DeLong, 2021; Englund et al., 2011; Rall et al., 2012; West & Post, 2016). As expected by previous results and theory, detection/handling times decreased with temperature (Figure 2c). Juveniles, however, evidenced a possible unimodal, convex relationship between temperature and space clearance rate, whereas previous results suggest that space clearance rates should increase or show a unimodal, concave relationship with temperature (DeLong, 2021; Englund et al., 2011; Rall et al., 2012; West & Post, 2016). As with juvenile feeding rates at high midge densities, this result may be due to a low number of surveys at high and low temperatures (survey temperatures ranged from 15.7°C to 44.7°C, but only 3 surveys were <20°C and 10 were >35°C). Alternatively, this temperature effect could be due to reduced escape ability by midges at high and low temperatures (Dell et al., 2014;

Kruse et al., 2008). Despite evidence for the effects of temperature on detection/handling times and, for juveniles, space clearance rates, we found little evidence of an effect of temperature on spider feeding rates overall. One possibility is that zebra jumping spiders can regulate their body temperature behaviourally, leading to an overall lack of a temperature effect (May, 1979). Spiders also may exhibit an activity response whereby they only forage over a range of suitable temperatures throughout the day, such that temperature has little effect on foraging rates during suitable times but foraging rates are zero outside of that temperature range. Last, temperature effects may not be strong enough to be detected given the variation among surveys in mean predator and prey sizes or by using the mean temperature of the wall as the measure of temperature for the survey.

The potential lack of short-term effects of temperature on feeding rates may have implications for the way in which we use temperature to predict how climate change alters predator–prey interactions. Previous studies predict a variety of potential responses of consumer–resource systems to increasing temperatures (Fussmann et al., 2014; Synodinos et al., 2021; Uszko et al., 2017; Vasseur & McCann, 2005). For example, studies are equivocal about whether warming should stabilize or destabilize predator–prey interactions (c.f. Fussmann et al., 2014; Vasseur & McCann, 2005). In a recent synthesis, Synodinos et al. (2021) showed how these results depend on specific assumptions about how parameters in consumer–resource models, including functional response parameters, change with temperature. However, if, as in our results, predator feeding rates show little response to temperature changes, then responses of consumer–resource systems may be more dependent on the temperature effects on other consumer and resource parameters such as conversion efficiencies and prey intrinsic growth rates (DeLong & Lyon, 2020). More realistic theory incorporating realistic temperature regimes and organismal responses to temperature combined with further estimates of the effect of temperature on predator feeding rates under natural conditions and over longer time frames will clarify how increases in temperature with climate change will influence consumer–resource interactions.

Predator densities generally reduce predator feeding rates (DeLong & Vasseur, 2011; Novak & Stouffer, 2021). Most studies on predator densities measure their effects by altering the densities of similar predators and examining the effects on average predator feeding rates (mutual interference). This has limited most previous studies from examining how intraspecific differences might influence interference rates. We found similar magnitudes of interference between females and juveniles. However, female feeding rates responded to total predator densities, while juveniles only responded to female predator densities, consistent with some previous suggestions (Sih, 1981). Although the exact mechanism of the negative effects of predator densities on feeding rates is not clear, we observed jumping spiders drawing the attention of one another and interrupting their foraging (i.e. wasted time). Juveniles may respond more strongly to females as they can be cannibalized by females (K.E. Coblentz; Personal Observation). This asymmetric interference among stages and sexes could have important consequences

for population dynamics, demographics and stage structure (Bassar et al., 2017; de Roos & Persson, 2013).

Although our results illustrate how observational approaches can provide insights into the factors shaping predator feeding rates in field settings, they also illustrate some of the difficulties. First, the observational approach employed here requires organisms with directly observable feeding events and measurable detection times, although this approach has been applied using stomach contents and the times in which prey are detectable in predator guts (Preston et al., 2018). Second, although using natural variation in conditions ensures that variables are within the range organisms experience, our results show that some conditions may be uncommon, leading to low sample sizes that may hamper inference. One solution to this would be to combine observational approaches and manipulative experiments (Coblentz et al., 2021; Novak et al., 2017). Third, as with any observational study, there is the potential for confounding effects that can influence the results. We hoped to minimize this by focusing on factors that were identified a priori as important for influencing predator functional responses. Fourth, the observational approach uses surveys of multiple individuals and therefore requires averaging across individual predator and prey body sizes and environmental conditions within a survey, limiting the ability to assess trait associations with the functional response parameters. Furthermore, the time frame of laboratory studies are generally long relative to the time organisms spend foraging, whereas our study focused on observable individuals actively foraging, and this may lead to differences in parameter estimates among the two methods (Coblentz & DeLong, 2021; Li et al., 2018). Despite the challenges to using this observational method, we are confident that future studies employing observational methods will provide important insights into predator functional responses under field conditions.

5 | CONCLUSIONS

Predator functional responses are shaped by a multitude of factors. However, our understanding of how these multiple factors might interact with one another to shape predator functional responses is limited by constraints to experimental approaches for measuring functional responses. Using a field-based observational approach, our results reveal variable effects of sexes/stages, temperature and interference on the functional response. Moreover, our results raise the possibility of a lack of temperature dependence in predator feeding rates under natural conditions and demonstrate asymmetric intraspecific interference. Further measurements of predator functional responses under field conditions will allow us to gain a better understanding of the multidimensional nature of predator functional responses and, therefore, a better understanding of predator–prey interaction strengths, their consequences and their responses to a changing climate.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

K.E.C. and J.P.D. designed the research; All authors performed the feeding surveys, K.E.C. performed the detection time observations, performed the statistical analyses and wrote the first draft of the manuscript. All authors contributed to revisions.

DATA AVAILABILITY STATEMENT

All data and code for their analyses are permanently archived on Zenodo <https://doi.org/10.5281/zenodo.6426222> (Coblentz, 2022).

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