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## Estimating predator functional responses using the times between prey captures

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**Abstract.** Predator functional responses describe predator feeding rates and are central to predator–prey theory. Ecologists have measured thousands of predator functional responses using the same basic experimental method. However, this design is ill-suited to address many current questions regarding functional responses. We derive a new experimental design and statistical analysis that quantifies functional responses using the times between a predators' feeding events requiring only one or a few trials. We examine the feasibility of the experimental method and analysis using simulations to assess the ability of the statistical model to estimate functional response parameters and perform a proof-of-concept experiment estimating the functional responses of two individual jumping spiders. Our simulations show that the statistical method reliably estimates functional response parameters. Our proof-of-concept experiment illustrates that the method provides reasonable estimates of functional response parameters. By virtue of the fewer number of trials required to measure a functional response, the method derived here promises to expand the questions that can be addressed using functional response experiments and the systems in which they can be measured. Thus, we hope that our method will refine our understanding of functional responses and predator–prey interactions more generally.

**Key words:** *exponential distribution; feeding rates; foraging; individual variation; jumping spiders; predator; predator–prey interactions; prey traits; time-to-event model.*

### INTRODUCTION

Predator functional responses are integral to ecological theory as they describe predator feeding rates given prey densities (Solomon 1949, Holling 1959a). Thus, functional responses are central to determining predator–prey interaction strengths, which in turn can determine species coexistence (Paine 1966, Holt 1977, Coblentz and DeLong 2020), the stability of ecological systems (Murdoch and Oaten 1975, McCann 2011), and other important characteristics of predator–prey interactions and food webs. It is no surprise, then, that ecologists have spent decades measuring thousands of functional responses (Uiterwaal et al. 2018). However, despite this effort, there remain many open questions that are difficult to address using the traditional functional response experimental design.

Most functional response experiments follow the same basic design. The experimenters choose a number of prey densities at which to measure foraging. The experimenters then add the specified number of prey to an arena generally containing a single predator individual and allow the predator to feed for a preallotted amount of time. After the allotted foraging time, the experimenters record the number of prey killed. This is repeated across all the prey densities multiple times typically using different predator individuals for each trial. The experimenters then fit a functional response model (s) to the data using one of several existing methods (e.g., Bolker 2008, Rosenbaum and Rall 2018, Uszko et al. 2020).

Although this same basic experimental design has worked for thousands of functional response experiments, it is ill-equipped to address several open questions regarding functional responses. For example, assessing the magnitude and ecological effects of intraspecific variation in functional response parameters is of great interest (Bolnick et al. 2011, Schröder et al. 2016). Using the current experimental design to measure

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an individual predator's functional response at five prey densities with three replicates at each prey density would require 15 trials with a single individual. This modest amount of replication and prey densities may quickly become infeasible for tens of individuals. Furthermore, for rare predators or prey it may be extremely difficult to collect enough individuals to be able to perform a standard functional response experiment. Another frontier in functional response experiments is understanding how predator and prey traits influence functional responses (Rall et al. 2012, Kalinkat et al. 2013, Uiterwaal and DeLong 2020). The link between morphology and behavior to the functional response is integral to understanding selection on both predator and prey, but including several levels of predator and prey traits can render experiments infeasible. This problem becomes more complicated because foraging interactions are determined by how predator and prey traits combine to influence strategies and the probability of successful attacks. For example, Kalinkat et al. (2013) examined the effects of predator and prey body sizes on the functional response across 25 predator species feeding on eight differently sized prey species requiring 2,564 experimental units. Finally, foraging rates depend on both abiotic and biotic conditions (Thompson 1978, Barrios-O'Neill et al. 2016, Preston et al. 2018, DeLong and Lyon 2020), so identifying the ways temperature, predator density, or habitat complexity influence the functional response generates the same level of replication challenge.

Here we derive an alternative experimental design and statistical analysis that uses a single predator individual and the time between its feeding events to measure its functional response. This method requires only one or a few trials to estimate an individual predator's functional response, easing some of the aforementioned difficulties with current functional response experimental designs. After deriving the method, we use simulations to show that this method performs well at estimating functional response parameters under many circumstances. We then present a proof-of-concept example with bold jumping spiders (*Phidippus audax*) foraging on adult midges (Chironomidae spp.).

#### *Derivation of the experimental method and statistical analysis*

An intuitive motivation for our method of estimating functional responses is an individual predator "feeding down" its functional response (Fig. 1A). As a predator feeds, it reduces the density of prey available. This fact was recognized long ago, and methods have been developed to account for prey depletion but not to capitalize on it (Royama 1971, Rogers 1972, Bolker 2008). As a predator feeds down its functional response, its feeding rate should also change according to the functional response. The question then becomes: Can we estimate the predator's functional response from observations of

the predator as it feeds on prey and depletes their number? The answer is yes, if we take advantage of the fact that the reciprocal of a rate is the expected time for an event to occur. Assume that the predator exhibits a Holling Type II functional response (as we will for the remainder of this manuscript, but see Appendix S3; Holling 1959a) in which the feeding rate  $f$  of the predator as a function of the resource density  $R$  is

$$f(R) = \frac{aR}{1 + ahR} \quad (1)$$

where  $a$  is space clearance rate of the predator (also known as attack rate or attack efficiency) and  $h$  is the handling time. Under this model, the expected time between feeding events is the reciprocal of the feeding rate, or

$$\frac{1}{f(R)} = \frac{1 + ahR}{aR} = \frac{1}{aR} + \frac{ahR}{aR} = \frac{1}{aR} + h. \quad (2)$$

Therefore, at prey density  $R$ , the expected time-to-feed for the predator is the expected time to encounter and catch a prey individual  $1/aR$  plus the time required to handle the previous prey ( $h$ ). If we watch a predator as it feeds across different prey densities and record the time between its feeding events, we should then be able to use the time-to-feed data to infer the predator's functional response parameters.

To derive a statistical method for estimating the functional response, we translate Eq. 2 into a stochastic process. First, we focus on the time to encounter and catch a prey individual ( $1/aR$ ). Stochastic process models show that times between encounters between individuals (e.g., predators and prey) are expected to be exponentially distributed (Dennis 1989). Thus, we can model the time to encounter and catch a prey individual at prey density  $R_i$  as exponentially distributed with  $\beta = aR_i$ , where  $\beta$  is the rate parameter of the exponential distribution. To extend this model from the expected time to encounter and catch a prey individual to the expected time between feeding events, we need to add the handling time. To do so, we recognize that the minimum time between feeding events is the handling time. Thus, we can alter the exponential distribution so that its minimum value is the handling time. Using this, we can model the time-to-capture  $y_i$  for a predator at prey density  $R_i$  as

$$y_i \sim \text{Exp}(\beta = aR_i)T(h, \infty) \quad (3)$$

where the tilde ( $\sim$ ) means "distributed as,"  $\text{Exp}$  denotes the exponential distribution, and  $T$  denotes that the distribution is truncated to the interval  $[h, \infty)$ . With a series of time-to-capture measurements across prey densities, one can use Eq. 3 to estimate  $a$  and  $h$  using Bayesian or maximum-likelihood methods (Bayesian methods are employed throughout the manuscript, but a maximum-likelihood approach is outlined in Appendix S2).

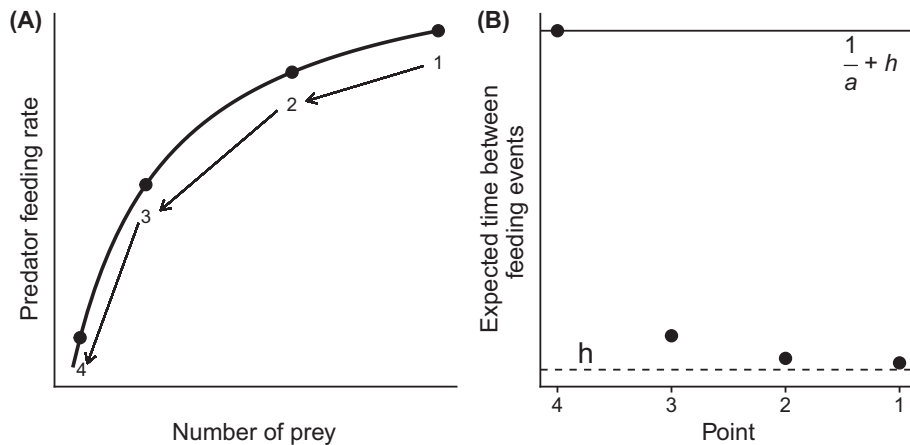


FIG. 1. As predators “feed down” their functional response, the number of prey decreases with the predator’s feeding rate according to the functional response (e.g., from points 1 → 2 → 3 → 4 in A). Likewise, at each number of prey available, the expected time between feeding events according to the functional response changes in a manner that provides information on the functional response parameters (B). The times between feeding events at high prey densities are particularly informative about the handling time ( $h$ , point 1), and times between feeding events at low prey densities are informative about the space clearance rate given the handling time ( $a$ , point 4R). The x-axis in panel B is reversed to match panel A.

To build intuition on how the time between feeding events allows us to infer the values of the space clearance rate and handling time, we consider two examples. First, assume that prey densities are very large. At large prey densities, the time to encounter and capture a prey item ( $1/aR$ ) is very small. Thus, the time between feeding events is approximately equal to the handling time (Fig. 1B). Alternatively, assume that there is only one prey item. The expected time-to-feed for the predator is  $(1/a) + h$  (Fig. 1B). So, given the handling time, the time-to-capture allows us to directly infer the space clearance rate. Therefore, by following the times between feeding events as a predator “feeds down” its functional response, we can estimate the functional response parameters. Furthermore, observations at high prey densities are particularly informative about the predator’s handling time, and observations at low prey density are particularly informative about the predator’s space clearance rate (see Discussion for an application to alternative experimental designs).

Although our derivation of this alternative experiment for measuring predator functional responses comes directly from the definition of the functional response, it is not a given that the statistical method will accurately estimate the functional response parameter values. To address this, we performed a simulation study in which we varied the functional response parameters, simulated time-to-capture data sets, and assessed how well the model was able to estimate the true functional response parameter values. We also performed a proof-of-concept experiment using bold jumping spiders feeding on midges to illustrate the use of this alternative experimental approach with real organisms. Overall, the simulations and experiment suggest the experimental approach outlined here is feasible for many organisms.

## MATERIALS AND METHODS

### Simulation study

We used simulations to examine the ability of the statistical model to estimate functional response parameters from time-to-capture data. For three space clearance rates ( $a = 0.003, 0.5, 50$ ), three handling times ( $h = 0.001, 0.01, 1$ ), and three initial prey densities (10, 25, 50), we simulated times between feeding events until all prey were consumed. At each prey density, the time-to-capture was simulated by drawing a random sample from an exponential distribution with rate  $\beta = \alpha R$  and adding the handling time. After simulating the data, we estimated the space clearance rates and handling times by fitting the model in Eq. 3 to the data in a Bayesian framework using the program ‘Stan’ (v. 2.21.0) through the package ‘RStan’ (v. 2.19.2) in R (v. 3.6.2) (Carpenter et al. 2017, R Development Core Team 2019, Stan Development Team 2019). We placed a Cauchy prior with location  $\mu = 0$  and scale  $\sigma = 5$  truncated at zero for the low and intermediate values of the space clearance rate and a Cauchy prior with  $\mu = 50$  and  $\sigma = 15$  truncated at zero for the highest value of the space clearance rate. For the handling time, we placed a Cauchy prior with  $\mu = 0$  and  $\sigma = 2.5$  truncated below at zero and above at the minimum observed time between feeding events (the minimum observed time between feeding is an upper limit on the handling time). These priors reflect the use of vaguely informative priors that we encourage given the number of previous functional response experiments. We performed 100 simulations for each space clearance rate, handling time, and initial prey density combination. After fitting the models, we determined (1) the proportion of simulations for which the true parameters were within the 95% credible

interval of the estimates, (2) the proportion of parameter point estimates that were greater than the true value (overestimated), and (3) the mean absolute difference between the point estimates and the true values. The range of parameters considered are well within those that have been observed in traditional functional response experiments (Uiterwaal et al. 2018).

#### *Empirical study—Bold jumping spiders*

As a proof-of-concept experiment, we used the time-to-capture method to estimate the functional responses of two bold jumping spiders (*Phidippus audax*) feeding on small adult midges (Chironomidae spp., average length 6.15 mm, SD = 1.2) collected from the outsides of buildings at the Cedar Point Biological Station (Ogallala, Nebraska, USA). We chose bold jumping spiders as predators because they are relatively common, yet previous attempts to measure their functional responses have failed because too few individuals could be collected to use one per trial as is standard in traditional functional response experiments. We chose midges as prey because they are a common prey item in bold jumping spider diets on the buildings from which they were collected (Okuyama 2007). After collecting the spiders, we kept the spiders in clear plastic vials and fed them 2–3 midges per day until the beginning of the time-to-capture trials. We collected midges daily to feed the spiders and for use in the time-to-capture trials. We maintained the lab in which the spiders were housed and the experiments performed at approximately 21°C.

To gather the time between capture data, we used a camera (HERO3, GoPro Inc., San Mateo, California, USA) to record video of the spiders foraging in a circular clear plastic arena 25 cm in diameter. For the first spider (Spider 1; 1.04 cm long including abdomen and cephalothorax), we performed three feeding trials on three consecutive days. We placed 3 prey in the arena in the first trial, 11 in the second, and 8 in the third. Spider 1 consumed all the prey in the first and third trials and 8 of the 11 prey in the second trial. For the second spider (Spider 2; 1.07 cm long including abdomen and cephalothorax), we also performed three trials on three consecutive days. We placed 3 prey in the arena for the first and second trials and 11 prey in the arena for the third trial. Spider 2 consumed all the prey in each of the trials. For each trial, we calculated the time between captures for each prey following the first capture, because by definition the time to capture for the first prey does not include handling time. Each spider had one observation for which it did not finish handling a prey before attacking the next one. As this is likely to bias the handling time estimates, we removed these observations prior to analysis. For the data from each spider separately and for the combined data across both spiders, we fit the exponential model in Eq. 3 in a Bayesian framework using the program Stan (v. 2.21.0) through the package ‘RStan’ (v. 2.19.2) in R (v. 3.6.2) (Carpenter et al. 2017, Stan

Development Team 2019). We placed a vaguely informative Cauchy prior with  $\mu = 10$  and  $\sigma = 10$  truncated at zero on the space clearance rate and a vaguely informative Cauchy prior with  $\mu = 0$  and  $\sigma = 2$  truncated below at zero and above at the minimum observed time between feeding events. The priors were derived from the FoR-AGE (functional responses from around the globe in all ecosystems) database using space clearance rates and handling times for invertebrate predators feeding on invertebrate prey (Uiterwaal et al. 2018). We perform a maximum-likelihood analysis in Appendix S2. All code and data can be found in Data S1 and Data S2.

## RESULTS

### *Simulation study*

Overall, the statistical model was able to estimate the functional response parameters well under most circumstances (Appendix S1: Table S1). However, the model struggled to estimate handling times when space clearance rates and handling times were low, exhibiting bad coverage of the credible intervals and overestimating handling times until reaching a space clearance rate of 0.5 and handling time of 0.01 (Appendix S1: Table S1; Fig. 2A, C). As space clearance rates increased, handling times were more accurately estimated across all levels of handling times considered (Appendix S1: Table S1; Fig. 2B, D). Coverage of the 95% credible intervals for the space clearance rates was near their nominal values for nearly all combinations of the variables, but the models showed a tendency to overestimate space clearance rates when they were low (Appendix S1: Table S1; Fig. 2). Estimates of space clearance rates and handling times improved with higher sample sizes (Appendix S1: Table S1).

### *Empirical Study—Bold jumping spiders*

For the time-to-capture data for both the individual spiders and the collated data across both individuals, the exponential model provided good fits to the data and reasonable estimates of space clearance rates and handling times (Fig. 3A). We estimated Spider 1's space clearance rate to be 6.5 m<sup>2</sup>/d (95% credible interval [CrI]: 3.6–10.9) and its handling time to be 0.0056 d (95% CrI: 0.004–0.0058). We estimated Spider 2's space clearance rate to be 14.0 m<sup>2</sup>/d (95% CrI: 6.25–25.8) and its handling time to be 0.0035 d (95% CrI: 0.0024–0.0037). Using the data from both spiders, we estimated a functional response intermediate between the two individual functional responses with a space clearance rate of 7.2 m<sup>2</sup>/d (95% CrI: 4.6–10.4) and a handling time of 0.0035 d (95% CrI: 0.00279–0.00367; Fig. 3B).

## DISCUSSION

Predator functional responses are an integral component of predator–prey theory and thousands of

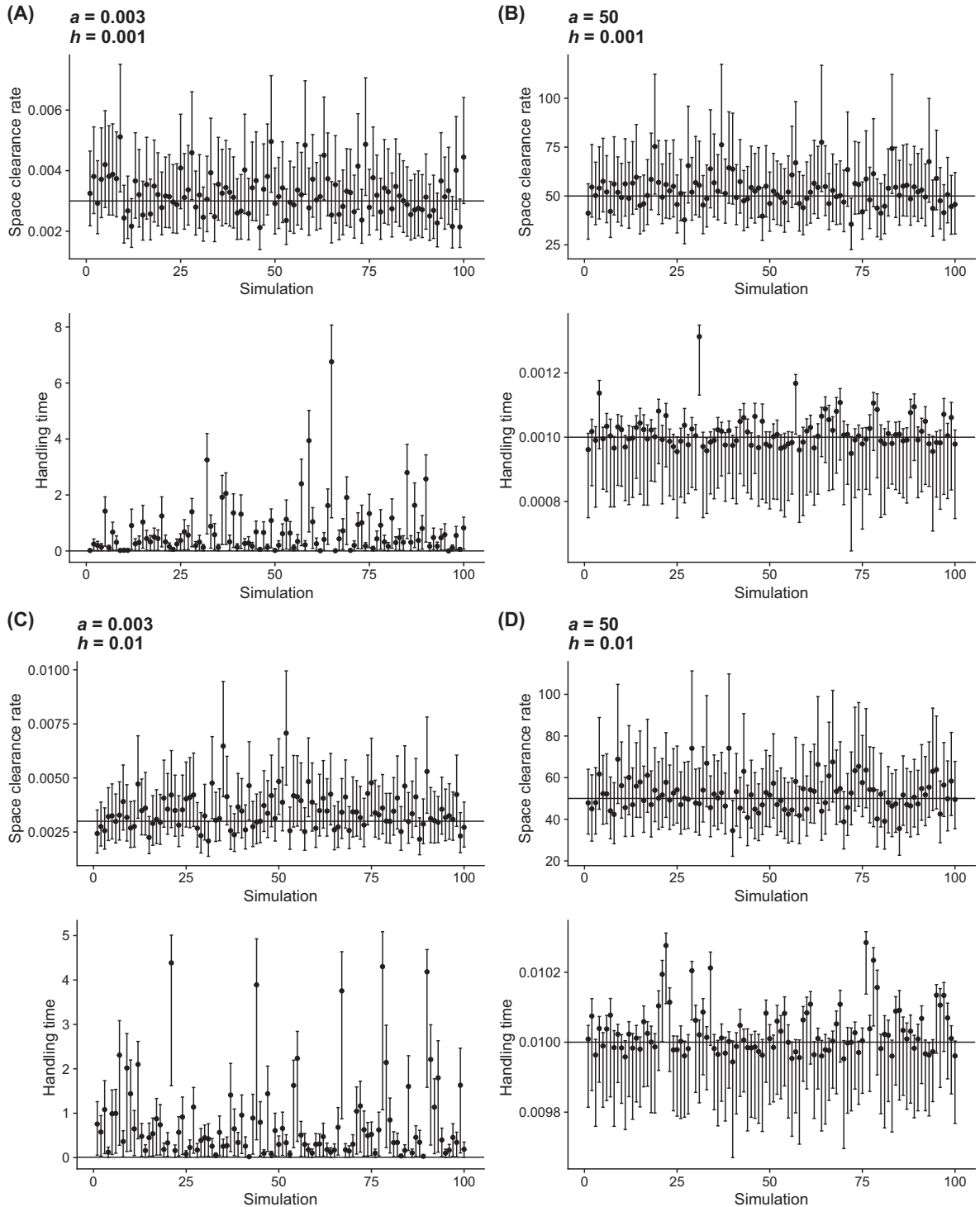


FIG. 2. The analysis of simulated time-between-prey capture data shows that space clearance rates ( $a$ ) are estimated well across a wide range of parameter values. The statistical method has difficulty estimating handling times ( $h$ ) when space clearance rates are small (A, C), but estimates handling times well at larger space clearance rates (B, D). For a summary of the simulation results, see Appendix S1: Table S1. These figures correspond to the results for the space clearance rates and handling times given in the figure and an initial prey density of 25.

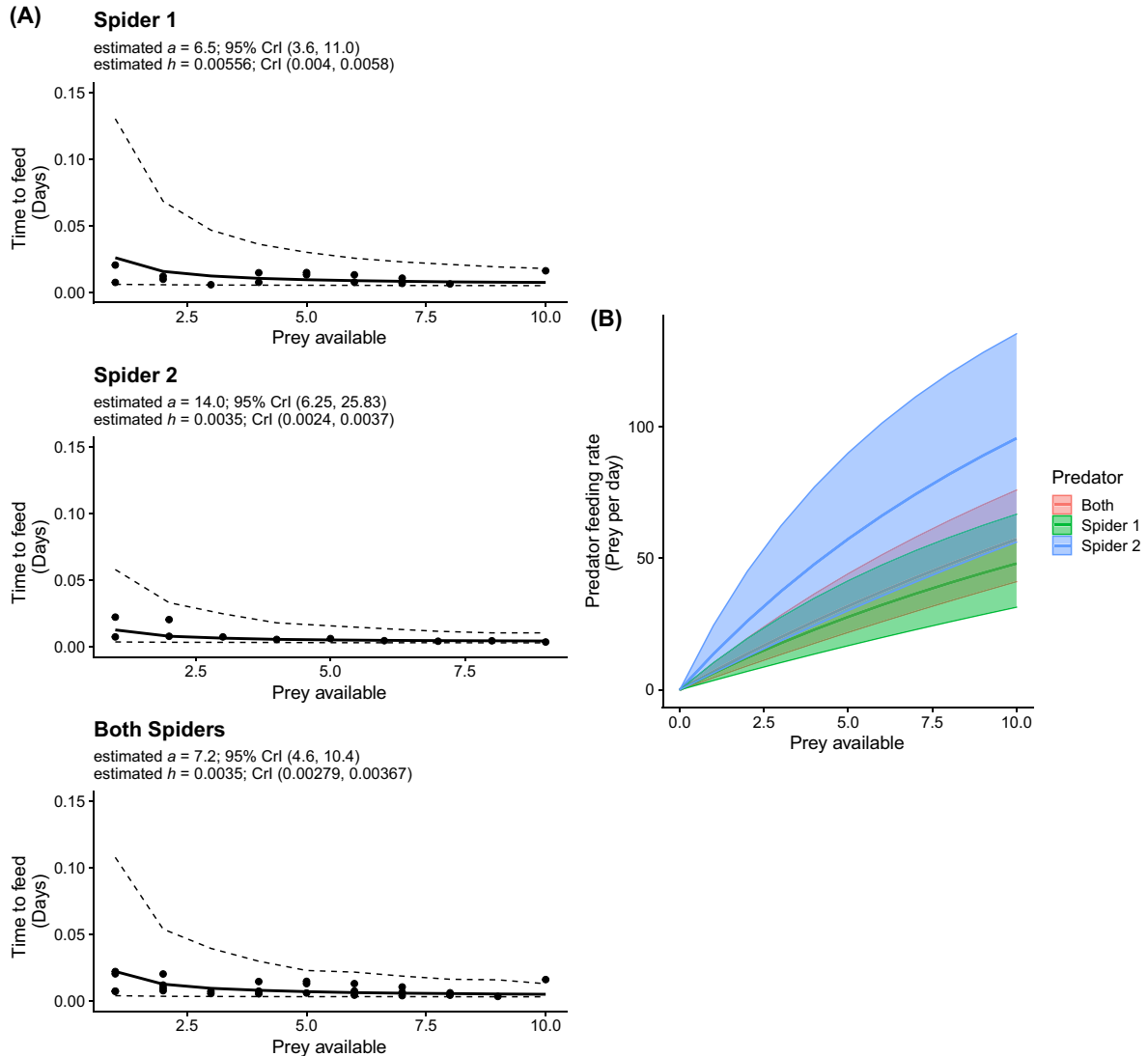


FIG. 3. The statistical model provided good fits to the time between prey captures and the number of prey available and reasonable functional response parameter estimates (A). The solid line in A is the expected relationship between the prey available and the time between prey captures. The dashed lines in (A) represent the 95% posterior predictive interval for the time between feeding events. The predicted functional responses (B) show generally higher feeding rates for Spider 2, lower feeding rates for Spider 1, and intermediate feeding rates for the combined data across both spiders (B). The colored areas in (B) represent 95% credible intervals (CrI) for the functional responses.

functional responses have been measured mainly using one traditional experimental design. This design has been effective, but it has also been limiting in terms of the systems to which it can be applied and its ability to address pressing questions such as intraspecific variation in functional response parameters and the role of traits in determining functional responses. We introduce an alternative method for estimating predator functional responses using the time between a predator's prey captures. Because this method requires only one or a few trials to estimate an entire functional response and can be used with individual predators, we believe it has the

potential to open several novel avenues of research on functional responses.

Although the time-to-capture method has potential for furthering the study of functional responses, it does face limitations. As with traditional functional responses experiments, the time-to-capture method also will be limited generally to species for which the experiments can be easily performed. However, the time-to-capture method is less constrained in terms of predators and prey that are rare, as fewer individuals are necessary to measure a functional response. Although this is possible because the time-to-capture method measures functional

responses at the individual level, researchers seeking to estimate population-level functional responses should ensure that the individual predators used are representative of the population. The simulation study also illustrates that the time-to-capture method is not likely to be able to estimate handling times well for species that have small space clearance rates. This is because small space clearance rates lead to long times between prey capture events even at high prey densities, which obscures the signal of handling times from the times between captures. The method also is unlikely to work for predators that continue to handle prey items as they attack and consume the next prey individual. As the handling time in the statistical model is the minimum amount of time between prey captures, the time-to-capture method is likely to underestimate handling times for predators that do not fully handle prey before capturing the next prey. Last, unlike modifications to traditional functional response experiments, the time-to-capture method is not likely to be applicable to herbivore or detritivore functional responses as the method depends on prey being discrete entities. Overall, the time-to-capture method is likely to be most appropriate for actively foraging species using starting prey densities for which the predator does not become satiated during foraging and for which consumption events are visible.

We derived the statistical method envisioning a predator feeding down its functional response and we used this method to estimate the jumping spider functional responses. However, the statistical analysis only requires time between captures at various prey densities to estimate the functional response parameters. This creates the potential for alternative experimental designs and applications to nonexperimental data. For example, for predators that consume prey slowly or become satiated quickly, one could focus on collecting the times between captures at very high and low prey densities. As previously mentioned, the times between prey captures at high and low prey densities are particularly informative about the predator handling times and space clearance rates, respectively. Furthermore, additional trials at high or low prey densities may help with parameter estimation even if the “feeding down the functional response” design is used. The statistical method here also may be used for observational data if the researcher is able to observe prey capture events and the densities of prey simultaneously. One intriguing application of this method to observational data is to carnivores or marine mammals outfitted with accelerometers. Previous studies have shown that these accelerometers can identify predation events (Viviant et al. 2014, Wang et al. 2015). If one can also estimate prey densities at the predator location, it may be possible to use the time between predation events to provide an estimate of the functional responses for predators not amenable to direct experimentation.

Although we focus on the Type II functional response, the time-to-capture method can be extended to other functional response types. For example, the Type III

functional response includes a so-called Hill exponent parameter allowing the functional response to take a sigmoidal shape (Real 1977). In Appendix S3, we use the same approach as in the main text to derive a statistical model for estimating Type III functional responses. Furthermore, the time-to-capture method also can be modified using additional data to address situations in which some of the assumptions of the model might be violated. For example, nearly all commonly used functional responses assume that the predator’s handling time is a constant. However, this assumption is likely to be violated if, for example, the time a predator spends handling a prey item is dependent on the density of prey available or predator satiation (Paterson et al. 2015). We show in Appendix S3 how this can be addressed if one is able to directly observe the times during which predators are visibly manipulating prey. We also show that the time-to-capture method can be used to infer, for example, the relationships between prey densities and handling times while estimating the functional response parameters. We hope future developments extend this method further and also modify it to address questions such as predator dependence in functional responses and the estimation of multispecies functional responses.

The functional response parameter estimates from the time-to-capture method are likely to differ from those estimated using traditional functional response experiments. In particular, we expect that the time-to-capture method will lead to higher estimates of space clearance rates and lower estimates of handling times than traditional functional response experiments. The parameters estimated using the time-to-capture method are akin to those in Holling’s original derivation of the Type II functional response or disc equation (Holling 1959*b*). Holling derived this equation assuming that all of a predator’s time was spent searching for or handling prey (Holling 1959*b*). In contrast, in most traditional functional response experiments, predators are placed in arenas for lengths of time that include not only active foraging by predators, but also periods of inactivity, satiation, hygiene-related activities, et cetera, that also decrease the time spent actively searching for prey. The time spent performing these additional activities alters estimates of functional response parameters leading to lower space clearance rates and longer handling time estimates (Jeschke et al. 2002, Li et al. 2017, Uszko et al. 2020). We predict that the larger the proportion of experimental duration spent foraging by the predator, the more similar the estimates from the two approaches will be. Whether one of these types of parameter estimates should be preferred over the other is likely to depend on the goal of the study. Surely, all predators spend some time performing activities unrelated to foraging and, thus, estimates including the time spent performing these activities may be more directly relevant to long-term feeding rates. However, in comparing functional responses say, among populations, estimates including the time spent performing activities other than

foraging makes it unclear what processes actually drive differences in functional response parameters. Thus, both types of estimates are likely to have a role in the study of functional responses, and translating between different estimates may eventually be possible with a better understanding of predator behavior.

#### CONCLUSIONS

Here we have introduced a method for estimating predator functional responses using the times between a predator's prey captures. This method is a promising addition to existing methods such as traditional functional response experiments and observational methods (Novak et al. 2017). Because this method requires only one or a few trials and can be performed on individuals, we believe this method can expand the questions one can ask using functional response experiments and the systems in which functional responses can be measured.

#### ACKNOWLEDGMENTS

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3307/supinfo>