Propagating uncertainty in ecological models to understand causation

Addicott *et al.* (2022) demonstrated that model selection via Akaike information criterion (AIC) may lead researchers to choose models in which the causal effects of focal variables are biased (Tredennick *et al.* 2021; Arif and MacNeil 2022). We agree that model selection approaches applied to a suite of correlative models are unlikely to provide causal inferences, particularly when researchers do not choose variables *a priori* to evaluate specific hypotheses. Rather, critical thinking about the focal system's causal structure (that is, "science before statistics"; McElreath 2020) is necessary. We appreciate the effort to bring this issue to the attention of the ecological community but wish to comment on the use of two-stage least squares in the analysis – in which point estimates of fitted values from one regression are used in a second regression as data – and highlight an alternative approach in which the uncertainty from the first stage is propagated to the second stage.

The authors simulated (see Addicott *et al.*'s [2022] Figure 1) fish population growth as a function of food (observed) and fishing effort (not observed). Catch (a proxy for effort) is observed but is confounded by growth rate. A naive model containing food and catch produces a biased effect of food but is "preferred" by AIC over a simpler – but unbiased – model containing only food. The authors evaluated a third approach in which the confounding variable (catch) is modeled as a function of food and the number of nets (an instrumental variable affecting catch but not growth rate). The resultant point estimates of catch (along with food) are then used in a second regression to estimate growth rate, leading to an unbiased estimate of food's effect. While this two-stage approach can be effective and is commonly applied, particularly in fields such as economics (Angrist and Krueger 1995; McElreath 2020), it does not propagate the uncertainty from the first stage to the second. Bayesian inference provides a solution: all parameters are viewed as random variables with associated uncertainty distributions, and thus unobserved latent variables can be incorporated with their uncertainty.

We replicated the authors' analysis in a Bayesian framework (considering three sample sizes: n = 25, 100, and 1000). In addition to their three models, we ran a modified version of their two-stage model in which uncertainty was propagated between the two regressions. The key feature of this fourth model is that the entire distribution of the fitted values for catch was used in the second regression, rather than a single point estimate. We wrote the models in the rstan version 2.26.9 interface to Stan (Carpenter *et al.* 2017). Code is available at https://github.com/n-a-gilbert/uncertainty and on Zenodo (Gilbert 2022). While such an approach could be pursued using a maximum likelihood framework (eg Besbeas *et al.* 2002; Bromaghin *et al.* 2010; Maunder and Punt 2013), it is typically more challenging to implement with standard software and likely to perform poorly for the small sample sizes common in ecological studies (Clark 2005; Royle and Dorazio 2008).

Propagating uncertainty in the two-stage approach resulted in more precise estimates of the focal effect at small sample sizes (Figure 1). At n = 25 and n = 100, the standard deviation of the food effect in the uncertainty model was 60% and 86%, respectively, of that from the model without uncertainty (Figure 1). At n = 1000, the standard deviation of the food effect in the uncertainty model was slightly larger (102%) than that from the model without uncertainty (Figure 1). Paradoxically, propagating uncertainty in such analyses may lead to more precise estimated effects when sample sizes are low. The model without uncertainty likely produces more uncertain results at the small sample sizes because the point estimates from the first stage are inaccurate. By more fully approximating the effect of catch, the model with uncertainty can better estimate the effect of food. However, ecological data are rarely as clean-cut as this simulation; propagating uncertainty in many, if not most, empirical settings likely avoids overconfidence in estimated quantities (Behney 2020).

Not propagating uncertainty in two-stage least squares is a specific case of omitting uncertainty in covariates. Regression analyses assume that covariates are measured without error. However,

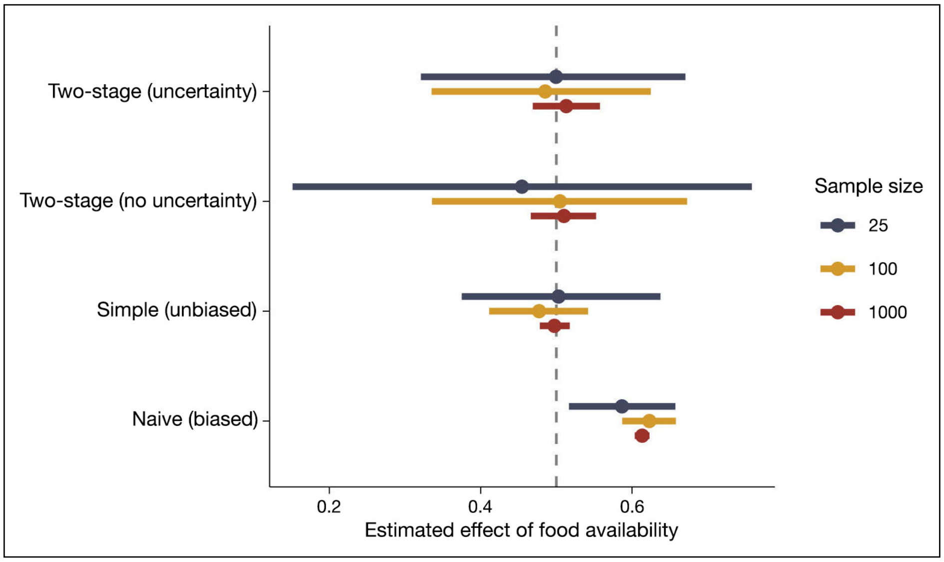

Figure 1. Estimated effects of food availability using Addicott *et al.*'s (2022) simulation, from four models run with three different sample sizes. Note the increased precision of the estimated effects for the two-stage model with uncertainty at low sample sizes. Solid circles are posterior means and bars are 95% credible intervals; the dashed vertical line is the true value of the effect.

researchers often measure variables (eg vegetation height) multiple times within a plot and then use the plot mean as a covariate (Behney 2020). The true mean is unobserved and thus uncertainty is lost when the sample mean is used. Behney (2020) found that Bayesian models accounting for uncertainty in a covariate generated less precise estimates of its effect than models that used site-level means of the covariate.

Importantly, not propagating uncertainty may have real-world implications if management or conservation decisions are made in accordance with the estimated effects of environmental variables on quantities such as abundance or occurrence (Walsh *et al*. 2012, 2015). Thus, omitting uncertainty in covariates may lead managers to take costly and time-intensive actions that are not merited (Behney 2020). Bayesian inference is becoming increasingly accessible (Monnahan *et al*. 2017), creating opportunities to adapt age-tested approaches – such as two-stage least squares – to propagate uncertainty and more thoroughly answer today's ecological questions.

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Reply to Gilbert, Eyster, and Zipkin

In their letter, Gilbert *et al*. apply a Bayesian framework to the motivating example in our paper *Toward an improved understanding of causation in the ecological sciences* (Addicott *et al*. 2022). Gilbert *et al*. concur with our central argument that understanding causal effects does not align with the burgeoning use in ecology of correlative model selection criteria such as the Akaike information criterion (AIC). They emphasize the need for "…critical thinking about the focal system's causal structure" and cite McElreath (2020) that "science before statistics" is necessary. While our arguments reflected the same emphasis on causal structure, we differ by adopting the American Statistical Association's assertion that good statistical practice is an essential component of good scientific practice (Wasserstein and Lazar 2016). We consider statistics and science inseparable when the goal is causal inference. Our primary focus was on generating plausibly accurate causal effect sizes, where we emphasize "plausibly accurate" because we acknowledge that truth in ecological systems will be unknowable.

Although precision is valuable, the heart of causal understanding is accuracy. We believe that Gilbert *et al*. would agree with this contention, given their agreement that information-theoretic methods are not tailored for identifying causal effect sizes. Indeed, we retrieved highly precise but inaccurate parameter estimates using AIC because the approach is blind to whether the system's causal structure is accurately resolved. Similarly, recent high-profile examples of the "Big Data Paradox" reflect how poor causal understanding can lead to precise but inaccurate estimates (Bradley *et al*. 2021). The common issue here is inaccurate causal understanding, where the inaccuracy is generated at the study design, measurement, or statistical analysis stages of the scientific process. Gilbert *et al*.'s comment addresses precision once a plausibly accurate causal effect has been identified.

The three arguments that Gilbert *et al*. advance about the precision of a plausibly accurate estimate are (1) that two-stage least squares analyses do not address measurement error, (2) that