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Niche Construction Through an Optimal Host Brood Size Is Supported in Brown-Headed Cowbirds: A Response to M. Soler

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1 | Introduction

Chicks of generalist avian brood parasites, who share the nest with host young, must balance the benefits that nestmates provide in eliciting care from (foster) parents against the costs incurred while competing for these provisions. In Antonson et al. (2022), we demonstrated that nestlings of the brown-headed cowbird (*Molothrus ater*), a generalist brood parasite, receive more food and survive best when reared with an intermediate number of host nestlings rather than with too many or none, in support of the begging assistance hypothesis (Kilner, Madden, and Hauber 2004; Figure 1). However, our results also provided evidence for a strategy beyond begging assistance, as we also demonstrated that nestling cowbirds on average reduced broods and fledged with only 2 host nestmates. Specifically, host broods were reduced when the cowbird hatched alongside 4 host hatchlings, but when experimentally hatched with 2 host hatchlings, brood sizes remained at this optimum. These results are consistent with a niche construction strategy whereby the nestling cowbird manipulates its social environment to increase its own probability of survival (Odling-Smee et al., 2013). Soler (2023) disagrees, and here we respond to his critique.

Soler's objection #1: That "the crucial prediction of the niche construction hypothesis—that is, that the cowbird nestling causes selective host brood reduction, allowing the survival of just two host nestlings—was not demonstrated."

In Antonson et al. (2022), we tested the hypothesis that brood reduction in larger-than-optimal brood sizes in nest boxes of prothonotary warblers (*Protonotaria citrea*) was directly attributable to the parasitic cowbird nestling. To do so, we used a paired experimental design whereby we experimentally generated parasitized and non-parasitized broods with the same number of nestlings at both the optimal or larger-than-optimal host brood sizes. We found that only larger-than-optimal broods *containing a cowbird nestling* experienced brood reduction (Figure 2).

Although this finding demonstrates that the presence of a brown-headed cowbird nestling causes brood reduction, Soler (2023) suggests that our experimental design was insufficient to demonstrate that brood reduction was due to any special adaptations on the part of the cowbird. Antonson et al. (2022), in Soler's (2023) opinion, should have included a 5th treatment where a warbler chick twice the size of the rest would have been fostered to ensure brood reduction was intrinsic to the parasitic

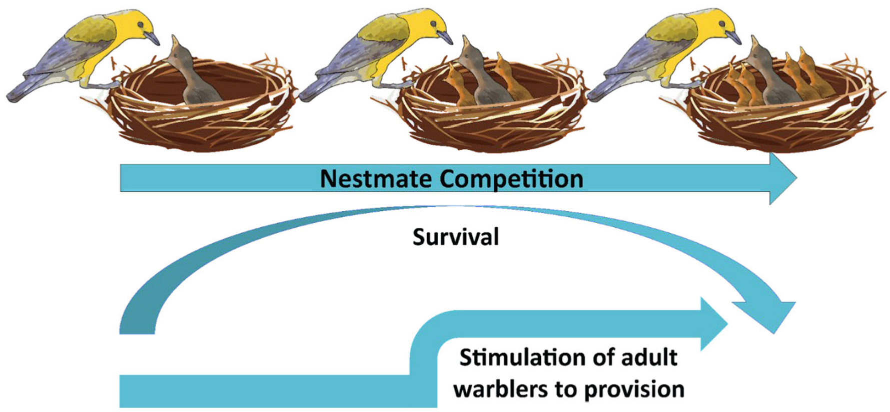

FIGURE 1 | Behavioral ecology of the niche construction model proposed and tested by Antonson et al. (2022). Nestling images adapted from wikiHow to Feed a Baby Bird CC BY-NC-SA 3.0 DEED.

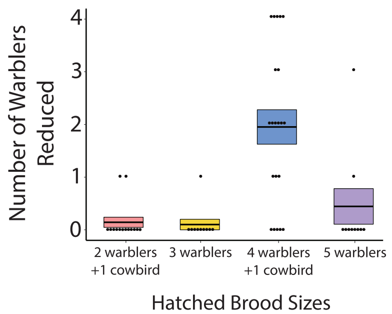

FIGURE 2 | Modified from Figure 3 Antonson et al. (2022) showing the paired experimental design demonstrating brood reduction only in large broods containing a cowbird. Boxes represent mean and standard error with individual data points represented.

species. Such a design, in Soler's (2023) view, would enable one to distinguish whether the brood reduction we observed was due to unique behavioral adaptations employed by the parasitic cowbird or simply a general outcome when any larger nestling is raised alongside several smaller warbler offspring.

Our view is that while this is an interesting point, it does not invalidate our original conclusions. We set out to test whether cowbirds cause host nestlings to die at a rate that would benefit parasitic survival and found evidence to support this hypothesis. We did not set out to test *how* cowbirds cause brood reduction nor whether brood reduction is *unique to cowbirds/brood* parasites. If that had been our goal, then Soler's suggested additional treatment would indeed have been essential, albeit infeasible due to vast differences in the developmental trajectories of cowbirds and prothonotary warblers.

Of relevance here are previous experimental studies, such as the one conducted by Hauber (2003). Here an older nestling, either a host chick or a brown-headed cowbird chick, was fostered into the broods of younger host Eastern phoebes (*Sayornis phoebe*), specifically to test whether brood reduction caused by cowbirds differed from brood reduction caused by equivalently large host nestlings. Hauber (2003) concluded that, while brood reduction was largely driven by a relatively large size, competitive features of the cowbird nestling were also necessary to explain all host nestling mortality. In our view, this previous study has already addressed the interesting question posed by Soler.

To some extent, evidence in the prothonotary warbler-cowbird literature supports a distinct effect of parasitism. For example, parasitized nests receive greater provisioning even when adjusting for brood mass (Hoover and Reetz 2006), and cowbirds have distinct effects on host parents and nestlings in terms of baseline corticosterone and immune response when compared with unparasitized broods of the same mass (Antonson et al. 2020a; Scharf et al. 2021).

Conclusion on Soler's Objection #1: While an interesting idea, to truly perform what Soler aspires for with the suggestion of this additional treatment (which has been performed previously in another cowbird host), one would actually need to add several different non-parasitic species that are the same size as a cowbird to the nests of a host (such as prothonotary warblers) and measure "parasite" survival and brood reduction. This would be the only empirical manner of addressing the concept of parasitic *uniqueness* in the adaptive nature of brood reduction, rather than a 5th treatment with developmental confounds. However, such an experiment would be an interesting follow-up to the one we have performed.

Soler's objection #2: That host species' relative body size is a relevant factor for the evolution of a niche construction adaptation which that was not discussed by Antonson et al. (2022).

We generally agree with Soler (2023) that when host nestlings are larger than a generalist brood parasite, there would be less opportunity for a niche construction strategy to evolve, due to the increased competitiveness of those host nestlings and a lack of support for the begging assistance hypothesis in those species. This is an extension of the earlier suggestion made by Kilner (2005), that host-tolerance by brood parasites is more likely to evolve when the brood parasite species is small relative to the host species. As such, we regard Soler's insights here as adding color to our conclusions, rather than indicating they are wrong. His ideas show how a niche construction strategy can be context-dependent and rest, at least in part, on the choice of host nest made by the adult female cowbird when parasitizing a host.

However, for the sake of this debate and to consider the role of host versus parasite body size, we would like to clarify a few interesting points made by Soler (2023) that are both ambiguous or rely on assumptions. These clarifications are important to address as they provide justification for cowbirds as a system by which a niche construction strategy through a general optimum could evolve in a nest-sharer brood parasite:

1. *Quantifying relative body sizes*: Soler (2023) never formally categorizes body size in his critique, referring only to the amorphous concept of "large hosts," "mid-size hosts," and "small hosts". It is unclear whether Soler (2023) defined these sizes himself or pulled them from the definitions of the studies cited in the critique. Formalizing these terms is critical not just for this debate, but more broadly for establishing operational body sizes for testing future questions related to parasitic niche construction. Here, we formalize the definitions of "Small Host," "Equal-sized Host," and "Large Host" as being less than 2 standard deviations (SD) smaller than the mean adult brown-headed cowbird mass, within ±2 SD of the mean ($\mu = 42.8$ g, 1 SD = 6.2 g, $n = 3990$), or more than 2 SD larger than the mean, respectively, using adult cowbird body mass that is based on 25+ years of cowbird banding data from the United States Geological Survey (USGS Bird Banding Laboratory 2023) to compare with mean host body size data (Birds of the World 2022; Myhrvold et al. 2015). Note: Under this definition, prothonotary warblers would be considered a small host.
2. *The assumption of which species cowbirds parasitize*: Soler's argument hinges on the idea that relatively larger body size of hosts would be a relevant factor that would prevent how niche construction could evolve in cowbirds. However, cowbirds are generalists that parasitize more than 200 species (Antonson et al. 2020b). If the majority of these host species are of a similar size or smaller than the cowbird itself, then the selection pressure would not exist to prevent the strategy. If cowbirds, however, parasitized larger hosts than themselves more regularly, as occurs in the great spotted cuckoo (*Clamator glandarius*) parasitic system that M. Soler regularly studies, then host body size would be a relevant selective pressure that may prevent the evolution of the niche construction strategy we propose in Antonson et al. (2022). We demonstrate, as illustrated by Figure 3A,B (Antonson et al. 2020b; Supporting Information Data 1), that clearly the former is true and cowbirds parasitize very few hosts larger than themselves, except in rare or non-adaptive instances (such as parasitic egg rejection).

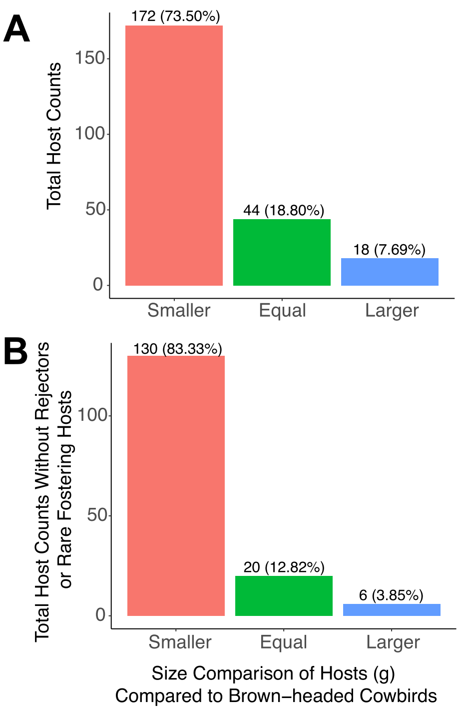

FIGURE 3 | Histograms using the number of hosts of brown-headed cowbirds in each size category. (A) Represents totals of all hosts, including those that reject cowbird eggs, while (B) represents the hosts where the selection pressure for a niche construction strategy is likely to exist.

While we feel that these data are already sufficient to counter the assumptions of Soler's host body size critique, we do wish to acknowledge that one limitation of these data is they do not incorporate measures of the adult parasite's host preference, which remains a long-standing question in brood parasitism research at large (see Strausberger and Ashley 1997; Woolfenden et al. 2003).

3. *The assumption that nestling body size is prohibitive to parasitic brood reduction in brown-headed cowbirds*: This argument also assumes that body size is a relevant trait for determining brood reduction and provisioning outcomes. A good deal of literature supports this point as Soler (2023) highlighted (particularly regarding foster-parental provisioning rules; e.g., Lichtenstein and Sealy 1997; Rivers, Loughin, and Rothstein 2010). However, in some large species, such as the Western meadowlarks (*Sturnella neglecta*; mean adult body mass = 97.7 g), a larger cowbird host species that is not a regular egg rejector, parasitized brood sizes at fledging were smaller with just 2.4 host nestlings versus 3.7 in non-parasitized nests (Davis 2003). This same publication also showed that parasitized clutches were on average 4.1 eggs as opposed to 5 eggs in non-parasitized nests. While this was not an experimental study, as we conducted in Antonson et al. (2022), these conditions were similar to our experimental design and demonstrate that host body size is not prohibitive to host brood reduction. Although an example from a single species, it provides evidence that it can happen, and further work should be conducted to determine whether these brood reduction patterns occur via the begging assistance hypothesis, partial predation, or some other mechanism such as early thermoregulation of the brood as suggested in Antonson et al. (2022).

Conclusion on Soler's Objection #2: This pattern of host size use is indeed important. The host species that cowbirds *actually* parasitize are likely not large enough to exert the strong selection pressure due to body size that Soler suggests would be prohibitive to the evolution of niche construction by this parasite's nestlings. Perhaps even more intriguing, this pattern provides further evidence that host species, generally similar in size or smaller, are intentionally selected by female cowbirds as part of the niche construction strategy for their offspring. Future research should explore patterns of parasitism across hosts within the niche construction framework.

Response to Soler's accusation of a citation bias:

The points made above and our knowledge of relative body size as a factor in brood reduction, which were well known by Antonson et al. (2022), are also more than sufficient to counter the accusation of selective citation levied by Soler (2023). This accusation by Soler implied either intention or ignorance by the authors of Antonson et al. (2022), so it is important to address that these papers were "excluded" not because of intention or ignorance but because of a lack of relevance to the brown-headed cowbird's ecology. All the "excluded" papers mentioned by Soler (2023) deal with systems where other brood parasitic species regularly parasitize hosts larger than themselves (Gloag et al. 2012; Bolopo et al. 2015; Soler and De Neve 2013), where the parasites are evictors and, therefore, irrelevant to our focal hypothesis (Martín-Gálvez et al. 2005; Hauber and Moskát 2008; Grim et al. 2009), or one study of brown-headed cowbirds where the experimental conditions were such that only one cowbird and one host nestling were in the nest together (Rivers, Loughin, and Rothstein 2010), which did not include simulating a natural host–parasite brood size condition as was done in Antonson et al. (2022). Of particular note, when Antonson et al. (2022) do refer to Gloag et al. (2012), it is cited for its relevance to the excellent theoretical model it presents in full support of a generalized niche construction strategy for brood parasites, rather than the accompanying experiment performed with a "large" and "small" host. Specifically, Gloag et al. (2012) reported provisioning and growth rates *of the parasite only* in two different host species and hence, host sizes. There is, in turn, no fitness-data on the survival of hosts, and parasites in these nests and thus their conclusions did not provide evidence for or against the conclusions of our study. They simply were within a different context. Thus, while we as the authors of Antonson et al. (2022) were fully aware of these studies when writing our own, this citation simply did not meet the criteria for mentioning in that context for our particular study, and we uniformly reject that this is bias and that "this bias in citing studies weakens the conclusions that can be drawn from this study".

2 | Addressing Soler's Question #1: How Could Such a Complex and Finely Tuned Adaptation Have Evolved in the Brown-Headed Cowbird?

This question by Soler (2023) stems from a misunderstanding or misrepresentation of Antonson et al. (2022). Antonson and colleagues never state that the niche construction that appears to occur in brown-headed cowbirds is finely tuned, and in fact the word "tuned" never appears in the original article. What *was* stated in Antonson et al. (2022) was, "Given the results of our survival analyses, future studies should consider how the timing of brood reduction by the cowbird in larger brood sizes affects their survival, as it is likely that the extent of brood reduction by cowbirds needs to be *finely timed and balanced* to not risk losing host aid in stimulating parents to provide sufficient care."

In actuality, we might argue against the *finely tuned* adaptation that Soler (2023) misstates that we support because of the general host use and relatively short evolutionary history of cowbirds as brood parasites. Rather, we would suggest a model like the one proposed by Gloag et al. (2012), where the "optimum in any one host is not necessarily equal to the optimum of another" as the most likely explanation for cowbird niche construction. Based on our data of cowbird host sizes, a generalizable strategy that works in the nests of smaller hosts is likely to be the strategy favored by selection simply due to the plethora of small hosts. That strategy may not be optimal for a cowbird reared in a large host's nest, but it may also not be necessary for cowbird survival if a larger host provisions larger prey items (Grim 2006) or a female cowbird more often punctures eggs in larger host species (Fiorini, Tuero, and Reboreda 2009). However, while we did not test nor state any aspect of niche construction as being finely tuned, we explore below the possibility of how generalizable the brood reduction strategy is, as it is an interesting question, and the data was easily obtained from two prior comparative analyses addressing similar questions (Hauber 2003; Kilner 2003; Supporting Information 2).

3 | Additional Evidence for Niche Construction and a General Optimum

In support of the niche construction proposed by Antonson et al. (2022), further support for a generally optimal host brood size exists for brown-headed cowbirds. Combining previously collated and published datasets (Supporting Information Data 2), we assessed published average survival-to-fledging data for cowbird chicks in the nests of a representative pool of host species (Hauber 2003; Kilner 2003). These results demonstrate that cowbird nestling survival in diverse host species' nests was best fitted by a quadratic regression (ΔAIC$=3.794$ improved fit over the linear model), suggesting that intermediate host brood sizes are a generalizable optimum for cowbird survival and broods of too many or too few host chicks are suboptimal for parasitic chicks (Figure 4A; $t_{2,20}=-2.394$, $p=0.027$, $R^2=0.642$), with peak cowbird survival at 2.21 host nestmates. This pattern matches that of prior comparative host data of optimal cowbird chick growth rates, which were also highest at intermediate brood sizes (Kilner, Madden, and Hauber 2004).

Further, we used these data to determine the average brood size for species when raised with or without a parasite. To do this, we used a linear mixed effects model with species as a random intercept. The numbers of host nestlings that fledge in naturally parasitized broods were significantly lower than the clutch or fledging brood sizes in non-parasitized nests of the same host species (Figure 4B; $F_{2,56}=121.1$, $p<0.001$) when compared with Tukey HSD *post hoc* tests. Together, these previously published lines of evidence suggest support for a general optimum for cowbird nestlings in the host brood sizes that are best for their growth and survival, as was proposed by the model of Gloag et al. (2012). These were the motivating comparative data that led us to hypothesize that, to cope with variability in the nests of diverse hosts, cowbird nestlings may alter host brood sizes through brood reduction as a niche construction strategy that would generate the rearing conditions optimal for parasitic young.

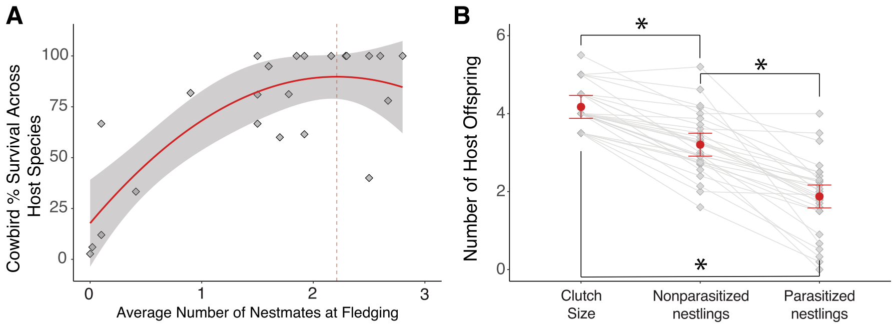

FIGURE 4 | (A) Cowbird survival to fledging across 23 host species follows a Goldilocks Principle of higher survival in an intermediate brood size compared to large or small brood sizes. Gray diamonds represent individual host species, and the quadratic regression line is represented in red with shaded confidence intervals. The red dashed line represents the inflection point in the quadratic regression line at $x = 2.21$ host nestmates at fledging. (B) The number of host offspring across 29 species decreases with advancing nest stage and differs between parasitism statuses. At fledging, non-parasitized brood sizes are significantly larger than parasitized brood sizes (clutch sizes are included for reference). Gray diamonds represent individual species, and gray lines connect individual species data points across groups. Red symbols with whiskers represent mean ± SE. Unlike the experimental data of Antonson et al. (2022), many of the studies included in this dataset were observational. Significant differences ($p < 0.05$) between groups after a Tukey post-hoc correction are represented in panel b by asterisks "*".

4 | Addressing Soler's Question #2: Is Multiple Parasitism Most Relevant to the Evolution of a Niche Construction Strategy?

Soler's (2023) final question revolves around the phenomenon of multiple parasitism. This is an interesting question; however, we feel it necessary to state that the data that Soler (2023) pulled from table 1 of Hoover (2003) do not represent the number of cowbird *nestlings* in parasitized nests as Soler states, but rather they represents the number of cowbird eggs per host clutch. This yielded a mistaken equivalence, as one of the major well-known effects of multiple parasitism of the same host nest is that it increases hatching failure with each additional parasitic egg in the clutch (Trine 2000; Goguen, Curson, and Mathews 2011). Instead, according to historical patterns and trends at our study sites, between 1994 and 2013 the average nest with a hatched cowbird nestling in our study area contained 1.31 cowbird chicks ($n = 1483$ nests), and has even declined more in recent years, with the average number of hatched cowbird nestlings between 2010 and 2013 being just 1.02 hatched cowbirds per parasitized nest ($n = 454$) (W. Schelsky and J. Hoover, unpublished data encompassing Hoover 2003) as mentioned by Soler) making the contemporary "typical" scenario to be one cowbird per warbler nest rather than multiple parasitism.

However, it is important to note that current trends do not represent evolutionary selective pressures (neither in our clarification nor Soler's original critique), so it was not investigated for our experiment. Rather, the goal of Antonson et al. (2022) was to specifically understand the reciprocal effect of a brood parasitic nestling and their host nestmates on one another. This is not to say that considering the role of multiple parasitism in the evolution of a niche construction strategy is not admirable. Indeed, multiple parasitism and even high parasitic relatedness can be locally very common (Rivers et al. 2012). When related to siblings sharing the nest, evidence suggests cowbirds may even reduce the intensity of their begging displays (Rivers and Peer 2016). In the context of niche construction, this could have numerous implications. First, if cowbirds actively modulate begging in response to kin, they may be able to do so in response to non-kin factors (such as host brood size) as well. Second, if suboptimal conditions such as competition (either by competitor size or brood size) modify growth or predation costs, then begging could be modulated by non-active factors as well. In either event, it is likely that multiple parasitism, where founded, could play a significant role in the evolution of niche construction strategy.

5 | Conclusion

Here we have clarified what we did and did not examine in Antonson et al. (2022). Although Soler has raised some interesting points, none of them challenge our central conclusions and instead build a basis for follow-up experiments. In doing so, these experiments would add nuance to our understanding of the complex biological interactions between the brown-headed cowbird and its many hosts. We have demonstrated in Antonson et al. (2022) that cowbirds can modify their social niche when parasitizing one host species. Addressing the questions here with follow-up experiments will determine *how* such a strategy and its coordination with host choice by adult parasites evolved, and by what mechanisms it is supported. We look forward to addressing those questions in the future.

Author Contributions

Nicholas D. Antonson: conceptualization, methodology, formal analysis, data curation, writing – original draft, visualization. **Wendy M. Schelsky:** supervision, writing – review and editing. **Deryk Tolman:** writing – review and editing. **Rebecca M. Kilner:** writing – review and editing. **Mark E. Hauber:** supervision, writing – original draft, writing – review and editing, formal analysis, conceptualization.

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Ethics Statement

This response only used previously published data. Therefore, no ethical approval for animal use was necessary.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code used in the analyses for this study are available at Figshare: https://doi.org/10.6084/m9.figshare.27642333.v1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.