1   *PERSPECTIVES*

2   The value of artificial stimuli in behavioral research:

3   Making the case for egg rejection studies in avian brood parasitism

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22   *Short title:* Artificial stimuli in egg rejection research

23

24   *Abstract*

25

26   Experimentation is at the heart of classical and modern behavioral ecology research. The

27   manipulation of natural cues allows us to establish causation between aspects of the

28   environment, both internal and external to organisms, and their effects on animals'

29   behaviors. In recognition systems research, including the quest to understand the

30   coevolution of sensory cues and decision rules underlying the rejection of foreign eggs by

31   hosts of avian brood parasites, artificial stimuli have been used extensively, but not without

32   controversy. In response to repeated criticism about the value of artificial stimuli, we

33   describe four potential benefits of using them in egg recognition research, two each at the

34   proximate and ultimate levels of analysis: (1) the standardization of stimuli for

35   developmental studies and (2) the disassociation of correlated traits of egg phenotypes used

36   for sensory discrimination, as well as (3) the estimation of the strength of selection on

37   parasitic egg mimicry and (4) the establishment of the evolved limits of sensory and

38   cognitive plasticity. We also highlight constraints of the artificial stimulus approach, and

39   provide a specific test of whether responses to artificial cues can accurately predict

40   responses to natural cues. Artificial stimuli have a general value in ethological research

41   beyond research in brood parasitism, and may be especially critical in field studies involving

42   the manipulation of a single parameter, where other, confounding variables are difficult or

43   impossible to control experimentally or statistically.   *Keywords*: artificial stimuli, brood

44   parasitism, egg rejection, recognition systems, research methods, unnatural

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Background

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50 Over 50 years ago, Niko Tinbergen performed classic experiments to determine whether egg

51 size and coloration affected avian parents' choices to incubate eggs or remove broken

52 eggshells and thereby reduce predation on nests (Tinbergen 1951, Tinbergen et al. 1962). By

53 testing competing predictions, drawn from alternative hypotheses at the same level of

54 analysis, Tinbergen endorsed and illustrated the value of the alternative hypothesis-testing

55 framework for evolutionary and mechanistic studies of animal behavior in the wild. A critical

56 component of these experimental approaches was the use of artificial stimuli that were

57 inspired by natural forms, but they either mimicked or exaggerated aspects of those

58 through the use of artificial materials (e.g., oversized model eggs, and brighter painted

59 colors, and artificially larger spots, than seen in natural eggs). In this way, the experiments

60 limited and defined both the modality and the degree of variation within and among egg

61 traits in order to best isolate those features that predictably elicited natural behaviors in

62 wild animals.

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64 Researchers have frequently and productively used painted model eggs, as well as dyed

65 natural eggs in the search for the recognition cues used by hosts of brood parasitic birds to

66 reject foreign eggs: well over 10,000 such egg rejection experiments have been completed

67 (reviewed in Grim 2007). In most of these studies, a model or painted-over natural 'parasitic

68 egg' is placed into an active nest and monitored for several days in order to determine

69 whether the egg is accepted, pecked, or ejected, or the nest is abandoned (e.g., Davies and

70 Brooke 1989, Antonov et al. 2009, Moskát et al. 2014).

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72 Yet, in recent years, both the value, and the general applicability of evolutionary conclusions

73 drawn about natural behaviors, through the use of artificial stimuli in egg rejection research,

74 have been repeatedly and openly questioned. Here, we define an artificial egg stimulus, as

75 any material and pigment that is not taken directly from nature; for example, according to

76 this definition, a natural or model egg dyed blue with a human-manufactured paint, to

77 resemble the avian-perception of the immaculate egg of an American robin *Turdus*

78 *migratorius*, is still an artificial stimulus (Croston and Hauber 2014). Accordingly, Honza and

79 colleagues (2007) used artificial dyes, to test the chromatic basis of foreign egg rejection by

80 song thrush *T. philomelos*. Avian visual modelling (Avilés 2008) was then applied to the

81 reflectance spectra of the artifial colors used, and combined with experimental rates of egg

82 rejection to characterize, for the first time, the sensory-perceptual basis of egg recognition

83 in birds (Cassey et al. 2008). Several studies followed these early works, including those

84 using conspecific eggs to characterize the fine scale perceptual cues causing egg rejection

85 behavior in other host species (e.g., Avilés et al. 2010, Spottiswoode and Stevens 2010,

86 Stevens et al. 2013a), but some of these also included pointed criticism that experiments

87 with artificial egg colors, and the resulting perceptual modelling, were not relevant to

88 evolutionary and ecological studies of brood parasitism in natural contexts. Recently, we

89 prepared a new manuscript inspired by Honza et al. (2007), and eventually published it (Bán

90 et al. 2013) but during peer-review, we repeatedly encountered several incarnations of a

91 knee-jerk reaction to our use of artificial stimuli to infer not only mechanistic but also

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92   evolutionary conclusions from the study. David Lahti's commentary (2014) in this journal

93   unpacks some of these concerns to complement our commentary below.

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95   We disagree with the premise and conclusion about whether artificial stimuli can be used to

96   explore evolutionary questions of brood parasites. Specifically, Tinbergen and his followers,

97   including ourselves, clearly recognize(d) that the mechanisms themselves are an evolved

98   phenotype that in turn influences the expression and outcome of selective pressures. Thus,

99   mechanistic and evolutionary questions are never uninformative about each other

100   (Taborsky 2014). Furthermore, for evolutionary studies aimed at understanding the causes

101   and consequences of natural variation of cues and responses, it is assumed and understood

102   that extant variation is the result of evolutionary forces that have constrained it (Samaš et

103   al. 2014). In turn, extending or exploring the phenotype's variable space beyond the natural

104   range is precisely what we need to do to probe how selection might be acting on novel

105   traits.

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107   Additionally, from an evolutionary perspective, whether a parasitic egg is rejected because it

108   is recognized as an egg or a non-egg (e.g., detritus, flower petal) in the nest cup, is

109   equivalent at the level of the fitness outcomes of responding to brood parasitism (i.e., egg

110   rejection: beneficial; egg acceptance: costly). In other words, no matter how and what hosts

111   perceive/interpret about the different objects (including eggs) that they see in the nest, the

112   only thing that matters from an ultimate/evolutionary perspective is the resulting fitness of

113   the host and the parasite. Conceptually, the same criticism can also apply for the use of a

114   natural, non-mimetic cuckoo egg: it, too, may be rejected because the host considers it a

115   piece of flower petal or other detritus fallen in the nest, or it may accepted it because its

116   appearance is so different from the hosts' own eggs so as to not be considered an egg, but

117   instead an integral nest construction material. What and whether artificial (and natural)

118   eggs placed into the nest are considered as "eggs" is an empirical question that requires

119   detailed and careful experimental analyses (reviewed by Guigueno and Sealy 2012) but

120   these questions should not be answered based on human (peer-reviewer's) *a priori*

121   interpretation of what a naturalistic stimulus should look like and what constitutes a

122   *'caricature of nature'*. If anything, recent brood parasitism research has taught us that over

123   the course a handful of decades, hosts can evolve brand new egg coloration to evade the

124   costs of accepting mimetic parasite eggs (Spottiswoode and Stevens 2012), thus what may

125   be a caricature today, might be reality tomorrow.

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127   To illustrate our argument in the context of the aims of ethological research, we highlight

128   four potential benefits of the use of artificial colors in the study of avian egg rejection

129   behaviors; critically, again, these benefits span both the ultimate and proximate levels of

130   analysis (Tinbergen 1963). We also use published data to illustrate to fellow researchers,

131   and to respond to critics, how to assess whether experiments with artificial stimuli may be

132   used to interpret natural variation in host responses to natural stimuli.

133

134   *Four potential benefits of artificial stimuli in egg rejection research:*

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136   **1. The standardization of stimuli for developmental studies, with a focus on repeatability**

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138   Individual hosts of brood parasites may consistently reject or accept naturally laid parasitic

139   eggs across repeated parasitism events, may switch from being acceptors to being rejecters,

140   (or vice versa), or may vary their responses based on other ecological cues. For example,

141   older oriental reed warblers *Acrocephalus orientalis* are more likely to reject common

142   cuckoo *Cuculus canorus* eggs than are younger warblers (Lotem et al. 1992). To understand

143   the ontogenetic basis of egg recognition and rejection, including its experience dependence,

144   and the roles of learning and maternal effects, requires experimentation with a

145   standardized set of stimuli across different time points of the host's lifespan (Samaš et al.

146   2011, Grim et al. 2014, Moskát et al. 2014). Because natural egg coloration changes within

147   days of laying in the nest (Moreno et al. 2011), as well as in storage under controlled

148   conditions (Cassey et al. 2010), and natural nests may be difficult to find in a timely manner

149   and the donor-species may be a protected or otherwise vulnerable taxon, it is not always

150   possible, and/or ethically justifiable, to use natural eggs as consistent stimuli for

151   developmental studies, including the study of repeatability. For example, repeatability

152   estimation requires the use of identical stimulus across repeated experiments with the same

153   individual; as any two natural eggs are never identical, the only way to test repeatability

154   robustly is through the use of artificial models (for details see Grim et al. 2014).

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156   **2. Disassociation of correlated phenotypic traits of eggs used for sensory discrimination**

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158   Once it has been established from observational and experimental studies whether and to

159   what extent hosts reject natural parasitic eggs, further use of natural eggs to understand the

160   sensory basis of egg recognition is a heuristically limited approach (de la Colina et al. 2012).

161 Natural stimuli often show limited variability overall in multidimensional trait space, but

162 exhibit extensive covariation between specific traits (e.g., avian feather colors: Stoddard

163 and Prum 2011); for example, eggs of brown-headed cowbirds *Molothrus ater,* that are

164 always rejected by American robins, are always smaller in size, beige in background, and

165 heavily maculated, compared to the larger and blue immaculate eggs of this host species

166 (Friedmann 1929). Any of these differing egg traits, or their combinations, may be the

167 possible recognition cue(s) for egg rejection, but these traits might simply be physiologically

168 or structurally constrained to co-vary. Thus, using natural cowbird eggs exclusively as egg

169 rejection stimuli prevents testing the relative contribution of size, color, and maculation in

170 American robin's egg recognition process (Rothstein 1982, Croston and Hauber 2014).

171 Instead, using unnatural combination of natural variation (e.g, small blue model eggs),

172 generates novel (artificial) models which can critically aid the characterization of the

173 proximate basis of the egg rejection cues used by hosts to eliminate parasitic eggs in the

174 nest.

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176 **3. The estimation of the strength of selection on parasitic egg mimicry**

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178 The rejection of parasitic eggs by hosts represents a critical selective pressure in the

179 coevolutionary arms race that drives parasites to evolve increasingly mimetic eggs, which

180 required increasingly fine-tuned sensory systems to be detected by hosts (Davies 2000). This

181 is because female parasites have nil fitness when their eggs are rejected and, thus,

182 represent an evolutionary dead end. Yet, some parasites lay highly mimetic eggs, many of

183 which are still rejected, whereas other parasites lay inaccurately or poorly mimetic eggs,

184   most of which are accepted (Stoddard and Stevens 2011). To characterize comparative

185   patterns of egg rejection behaviors, and to reconstruct the evolutionary trajectories of how

186   rejection behaviors have changed with exposure to brood parasitism, requires a

187   standardized metric of egg rejection responses (Grim et al. 2011). These, by definition,

188   cannot be based on responses to natural parasitic eggs, because the coevolutionary

189   hypothesis assumes a reciprocal and dynamic process between hosts and parasites, which

190   will result in varying degrees of host-brood parasite egg mimicry across different systems

191   (Igic et al. 2012). Instead, using a specific, variably rejected model egg color, can provide a

192   metric of egg rejection directly comparable across host populations and species.

193   Accordingly, analyzing the responses of different species of common cuckoo hosts in Europe

194   against the same artificial egg color, revealed that more discriminating and rejecting hosts

195   are parasitized by perceptually more mimetic parasite eggs (Stoddard and Stevens 2011).

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197   **4. Establishment of the evolved limits of sensory and cognitive plasticity**

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199   Presenting hosts exclusively with foreign eggs that are within the natural range of variation

200   can also lead to incorrect conclusions about whether hosts recognize and reject foreign

201   eggs. For example, some hosts, including the common redstart *Phoenicurus phoenicurus*

202   accept virtually all naturally laid parasitic common cuckoo eggs (Rutila et al. 2006). When

203   experimentally testing such a host's egg discrimination ability by introducing natural

204   parasite eggs laid elsewhere, model eggs painted to resemble them, or host eggs only

205   partially dyed, this host accepts most of these foreign egg types, too (Rutila et al. 2002,

206   Hauber et al. 2014). The results would then lead to the conclusion that egg rejection as a

207 defence against parasites has not evolved in the redstart. However, there is a biologically

208 critical, alternative functional explanation: that even if such hosts have evolved sensory

209 mechanisms to recognize increasingly similar foreign eggs, their recognition mechanisms

210 may be circumvented by the high accuracy of the coevolved mimicry of the parasitic egg's

211 appearance; in other words, the cuckoo eggs are such a good match of the redstart eggs

212 that they cannot be discriminated and, thus, rejected by this host. This alternative

213 hypothesis can be directly tested solely through the use of artificial eggs that deviate in a

214 known direction from the phenotypic range of natural host and parasite eggs; using natural

215 eggs of other species, or even conspecifics, would introduce both tractable (measured) and

216 intractable (unmeasured) sources of variation. Once the host's ability to reject such non-

217 matching eggs has been established, experimenters can move onto the use of better

218 matching (more mimetic) eggs in order to meaningfully isolate more proximate drivers of

219 egg rejection. Similarly, most of the grassland passerines that lay beige and spotted eggs,

220 accept all or nearly all beige and spotted cowbird-like eggs, but reject blue model eggs

221 (Klippenstine and Sealy 2008). Importantly, in hosts that do reject non-mimetic eggs, the use

222 of increasingly mimetic models is needed to establish the sensory thresholds of these

223 discrimination abilities, and then to test whether these perceptual acceptance thresholds

224 function adaptively, i.e. allow the rejection foreign eggs to reduce the fitness costs of brood

225 parasitism (e.g. Croston and Hauber 2014).

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227 *Responses to artificial stimuli can predict behaviors in response to natural stimuli: the case of*

228 *egg rejection by a brood parasite host*

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230   We recognize here that the use of artificial colors and/or materials can also be a severe

231   constraint on the utility of these experiments in evolutionary interpretations of egg

232   rejection data, for example when using treatments which only change the color of the egg in

233   spectral ranges not perceived by the subject (Avilés et al. 2006), or when model eggs are

234   made from materials that cannot be pierced or grasped for successful ejection, despite

235   repeated rejection attempts by hosts (Antonov et al. 2009). Nonetheless, to evaluate our

236   specific claim that, contrary to our critics, experimentally induced behaviors in response to

237   artificial stimuli can help to explain both causation and pattern in fitness-relevant responses

238   to natural cues, we focused on our own published data (Bán et al. 2013, Moskát et al. 2014).

239   Specifically, we tested for a predictive relationship between the evolved behavior (egg

240   ejection) and the artificial stimuli (dyed egg colors) at nests of the free-living great reed

241   warblers *Acrocephalus arundinaceus,* an intermediate rejecter host species of the common

242   cuckoo *Cuculus canorus* in central Hungary (Bán et al. 2013). From that study, we obtained

243   host responses to experimental parasitism with a single foreign egg (host egg dyed with a

244   highlighter pen of one of five colors, n = 12-16 nests), and contrasted them with egg

245   rejection rates of a natural conspecific egg (moved a different host's nest, n = 16; Bártol et

246   al. 2002), and a natural parasite egg (a cuckoo egg moved from a parasitized to a non-

247   parasitized nest, n = 13 nests; C. Moskát, unpublished data). We then calculated a stimulus

248   metric that can be applied to both artificial and natural color stimuli: we measured avian-

249   visible spectral reflectance (300-700 nm), and used perceptual modelling to estimate

250   chromatic contrast distances between natural host eggs' background coloration and

251   stimulus egg coloration (Moskát et al. 2014).

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253   Our data points did not include the limits of rejection probabilities (0%, 100%), and so we

254   used a linear regression analysis between egg rejection rates and pairwise just noticeable

255   differences (chromatic JNDs, n = 8 randomized egg-pairs per color type; Fig. 1); the result

256   showed a significantly positive relationship between perceivable chromatic contrasts and

257   egg rejection rates (R^2 = 0.29, $F_{5, 38}$ = 15.3, P = 0.0004). When we also plotted the mean

258   values of JNDs and experimentally induced rejection rates of single, natural conspecific eggs

259   or single, natural parasitic eggs amongst the data points from these artificial colors, the

260   natural eggs fell within the 95% confidence interval of the predicted means (Fig. 1); the

261   combined model, including both artificial and natural eggs, was also significant (R^2 = 0.32,

262    $F_{6,45}$ = 20.7, P < 0.0001). The implication is that behavioral responses to natural stimuli are

263   within the range predicted by variation in behavioral responses elicited by diverse artificial

264   stimuli.

265

266   *Conclusions*

267

268   Conceptually, our arguments go far beyond studies on egg rejection by hosts of avian brood

269   parasites, as similar dyeing treatments are also used for experimental studies on nest

270   predation (Weidinger 2001), nest mate recognition (Tibbetts 2002), and in many other

271   experimental fields of animal ecology, evolution, and behavior (Ferrari et al. 2008). For

272   example, artificial stimuli that fall far outside of range of natural stimuli proved to be useful

273   in non-brood parasitism studies, e.g., camouflage (Stevens et al. 2013b) and sexual selection

274   (Safran et al. 2010). Here, we argue that experimental studies with wild animals should not

275   be classified *a priori* as strictly mechanistic, and discarded as irrelevant to fitness, on the

276 basis that manipulations involve artificial stimuli in quantity, in quality, or in both. Instead,

277 artificial stimuli should be appreciated and utilized when these allow for the careful design,

278 alteration, and delivery of exact cues and triggers that elicit fitness-relevant responses in

279 freely behaving animals. This is especially relevant for studies in the wild, where other social

280 and ecological cues and contexts are typically uncontrolled, and most also remain

281 unmeasured. In turn, the possibility to design specific stimulus types that vary (only) along

282 known trait dimension(s), remains the core strength of behavioral experimentation.

283 Implementing diverse, and yet standardized stimuli can be informative for both proximate,

284 mechanistic questions about developmental and cognitive processes, and for ultimate,

285 comparative analyses of predicted behavioral responses induced by these stimuli, and their

286 consequences on fitness. However, we also recognize that there are limits to the use and

287 utility of artificial stimuli in the study of evolutionary processes (see Lahti 2014

288 commentary). To address these concerns empirically, we recommend (and illustrate above)

289 the use of statistical checks to assess whether chosen stimuli, and/or the behavioral

290 responses elicited by these, fit or predict the known range of responses elicited by natural

291 stimuli.

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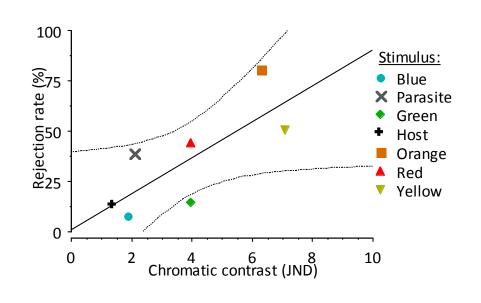307   *Figure 1.* The relationship between egg rejection rates of great reed warblers in response to

308   experimentally introduced eggs, and avian perceivable distances (chromatic JNDs) between

309   natural coloration of the host's own eggs and the artificial coloration of artificially dyed

310   natural eggs, as well as of natural conspecific and natural parasitic, common cuckoo eggs.

311   The graph depicts the mean JND and the percent of rejection per egg type, the regression

312   line (solid), and its 95 % confidence intervals (dotted lines).

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317   *References:*

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