1   *PERSPECTIVES*

2   The value of artificial stimuli in behavioral research:

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

4

5   Márk E. Hauber[1], Lainga Tong[1], Miklós Bán[2], Rebecca Croston[1], Tomáš Grim[3], Geoffrey I.N.

6   Waterhouse[4], Matthew D. Shawkey[5], Andrew B. Barron[6], and Csaba Moskát[7]

7   [1]Department of Psychology, Hunter College and the Graduate Center of the City University

8   of New York, 695 Park Avenue, New York, NY 10065, USA; email for correspondence:

9   mark.hauber@hunter.cuny.edu

10   [2]Department of Evolutionary Zoology, MTA-DE "Lendület" Behavioural Ecology Research

11   Group, University of Debrecen, Egyetem tér 1, Debrecen H-4032, Hungary

12   [3]Laboratory of Ornithology and Department of Zoology, Palacky University, 17. listopadu 50,

13   771 46, Olomouc, Czech Republic

14   [4]School of Chemical Sciences, University of Auckland, PB 92019, Auckland, New Zealand

15   [5]Department of Biology and Integrated BioScience Program, Box 390, Univerity of Akron, OH

16   44325, USA

17   [6]Department of Biological Sciences, Macquarie University, 209 Culloden Drive,

18   Sydney, NSW 2109, Australia

19   [7]MTA-ELTE-MTM Ecology Research Group, Hungarian Academy of Sciences, c/o Biological

20   Institute, Eötvös Lóránd University and Hungarian Natural History Museum, Pázmány Péter

21   sétány 1/C., Budapest, 1117, Hungary

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

45

46

47

48 *Background*

49

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.

63

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).

71

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

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.

94

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.

106

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.

126

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:*

135

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

137

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).

155

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

157

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.

175

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

177

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).

196

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

198

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).

226

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

228   *egg rejection by a brood parasite host*

229

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).

252

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
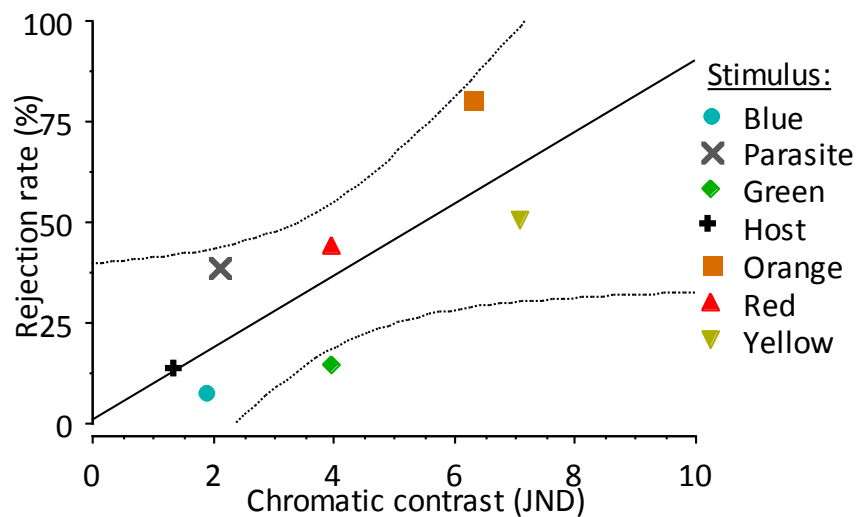
291   stimuli.

292

293   *Acknowledgments*

294

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).

313

314

315

316

317   *References:*

318

319   Antonov A, Stokke BG, Mosknes A, Røskaft E 2009. Evidence for egg discrimination

320   preceding failed rejection attempts in a small cuckoo host. Biology Letters 5: 169-

321   171.

322   Avilés JM 2008. Egg color mimicry in the common cuckoo *Cuculus canorus* as revealed by

323   modelling host retinal function. Proceedings of the Royal Society of London B 275:

324   2345-2352.

325   Avilés JM, Soler JJ, Pérez-Contreras T, Soler M, Møller AP 2006. Ultraviolet reflectance of

326   great spotted cuckoo eggs and egg discrimination by magpies. Behavioral Ecology 17:

327   310-314.

328   Avilés JM, Vikan JR, Fossøy F, Antonov A, Moksnes A, Røskaft E, Stokke BG. 2010. Avian

329   colour perception predicts behavioural responses to experimental brood parasitism

330   in chaffinches. Journal of Evolutionary Biology 23: 293-301.

331   Bán M, Moskát C, Barta Z, Hauber ME 2013. Simultaneous viewing of own and parasitic eggs

332   is not required for egg rejection by a cuckoo host. Behavioral Ecology 24: 1014-1021.

333   Bártol I, Karcza Z, Moskát C, Røskaft E, Kisbenedek T 2002. Responses of great reed

334   warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of

335   a cuckoo *Cuculus canorus* dummy and egg mimicry. Journal of Avian Biology 33: 420-

336   425.

337   Cassey P, Honza M, Grim T, Hauber ME 2008. The modelling of avian visual perception

338   predicts behavioural rejection responses to foreign egg colours. Biology Letters 4:

339   515-517.

340   Cassey P, Maurer G, Duval C, Ewen JG, Hauber ME (2010) Differential impacts of time since

341   collection on eggshell colour components relevant to perceptual modeling in

342   museum collections of song thrush (*Turdus philomelos*) eggs. Behavioral Ecology and

343   Sociobiology 64: 1711–1720.

344   Croston R, Hauber ME 2014. Spectral tuning and perceptual differences do not explain the

345   rejection of brood parasitic eggs by American robins (*Turdus migratorius*). Behavioral

346   Ecology and Sociobiology 68: 351-362.

347   Davies NB 2000. Cuckoos, cowbirds and other cheats. Poyser, London.

348   Davies NB, Brooke MDL 1989. An experimental study of co-evolution between the cuckoo,

349   Cuculus canorus, and its hosts. I. Host egg discrimination. Journal of Animal Ecology

350   58: 207-224.

351   de la Colina MA, Pompillo L, Hauber ME, Reboreda JC, Mahler B 2012. Different recognition

352   cues reveal the decision rules used for egg rejection by hosts of a variably mimetic

353   avian brood parasite. Animal Cognition 15: 881-889.

354   Ferrari MCO, Messier F, Chivers DP 2008. Can prey exhibit threat-sensitive generalization of

355   predator recognition? Extending the predator recognition continuum hypothesis.

356   Proceedings of the Royal Society of London B 275: 1811-1816.

357   Friedmann H 1929. The cowbirds: a study in the biology of social parasitism. Charles C.

358   Thomas, Springfield, IL.

359   Grim T 2007. Equal rights for chick brood parasites. Annales Zoologici Fennici 44: 1-7.

360   Grim T, Samaš P, Moskát C, Kleven O, Honza M, Moksnes A, Røskaft E, Stokke BG 2011.

361   Constraints on host choice: why do parasitic birds rarely exploit some common

362   potential hosts? Journal of Animal Ecology 80: 508-518.

363   Grim T, Samaš P, Hauber ME (2014) The repeatability of avian egg ejection behaviors across

364   different temporal scales, breeding stages, female ages and experiences. Behavioral

365   Ecology and Sociobiology 68: 749-759.

366   Guigueno MF, Sealy SG (2012) Nest sanitation in passerine birds: implications for egg

367   rejeciton in hosts of brood parasites. Journal of Ornithology 153: 35-52.

368   Hauber ME, Moskát, C, Bán M 2006. Experimental shift in hosts' acceptance threshold of

369   inaccurate-mimic brood parasite eggs. Biology Letters 2: 177-180.

370   Hauber ME, Samaš P, Anderson MG, Rutila J, Low J, Cassey P, Grim T (2014) Life-history

371   theory predicts host behavioural responses to experimental brood parasitism.

372   Ethology Ecology & Evolution (online).

373   Honza M, Polacikova L, Procházka P 2007. Ultraviolet and green parts of the colour

374   spectrum affect egg rejection in the song thrush (*Turdus philomelos*). Biological

375   Journal of the Linnean Society 92: 269-276.

376   Igic B, Cassey P, Grim T, Greenwood DR, Moskát C, Rutila J, Hauber ME 2012. A shared

377   chemical basis of avian host-parasite egg colour mimicry. Proceedings of the Royal

378   Society of London B 279: 1068-1076.

379   Klippenstine DR, Sealy SG 2008. Differential ejection of Cowbird eggs and non-mimetic eggs

380   by grassland passerines. Wilson Journal of Ornithology 120: 667-673.

381   Lahti D (2014) The limits of artificial stimuli in behavioral research: the umwelt gamble.

382   Ethology (this issue).

383   Lotem A, Nakamura H, Zahavi A 1992. Rejection of cuckoo egg in relation to host age: a

384   possible evolutionary equilibrium. Behavioral Ecology 3: 128-132.

385   Moreno J, Lobato E, Morales J 2011. Eggshell blue-green colouration fades immediately

386   after oviposition: a cautionary note about measuring natural egg colours. Ornis

387   Fennica 88: 51-56.

388   Moskát C, Takasu F, Muñoz RA, Nakamura H, Bán M, Barta Z 2012. Cuckoo parasitism on

389   two closely-related *Acrocephalus* warblers in distant areas: a case of parallel

390   coevolution? Chinese Birds 3: 320-329.

391   Moskát C, Zölei A, Bán M, Elek Z, Tong L, Geltsch N, Hauber ME 2014. How to spot a

392   stranger's egg? A mimicry-specific discordancy effect in the recognition of parasitic

393   eggs. Ethology 120: 616-626.

394   Moskát C, Bán M, Hauber ME 2014. Naïve hosts of avian brood parasites accept foreign

395   eggs, whereas older hosts fine-tune foreign egg discrimination during laying.

396   Frontiers in Zoology 11: 45.

397   Rothstein SI 1982. Mechanisms of avian egg recognition: which egg parameters elicit

398   responses by rejector species? Behavioral Ecology and Sociobiology 11: 229-239.

399   Rutila J, Latja R, Koskela K 2002. The Common Cuckoo *Cuculus canorus and* its cavity nesting

400   host, the Redstart *Phoenicurus phoenicurus*: a peculiar cuckoo–host system? Journal

401   of Avian Biology 33: 414-419.

402   Rutila J, Jokimäki J, Avilés JM, Kaisanlahti-Jokimäki ML 2006. Responses of currently

403   parasitized and unparasitized common redstart (*Phoenicurus phoenicurus*)

404   populations against artificial cuckoo parasitism. Auk 123: 259-265.

405   Safran RJ, Vitousek MN, Hauber ME, Ghalambor CK 2010. Sexual selection: a dynamic state

406   of affairs. Trends in Ecology and Evolution 25: 429-430.

407   Samaš P, Hauber ME, Cassey P, Grim T 2011. Repeatability of foreign egg rejection: Testing

408   the assumptions of co-evolutionary theory. Ethology 117: 606-619.

409   Samaš P, Hauber ME, Cassey P, Grim T 2014: The evolutionary causes of egg rejection in

410   European thrushes (*Turdus* spp.): a reply to M. Soler. Frontiers in Zoology 11: 72.

411   Spottiswoode CN, Stevens M 2010. Visual modeling shows that avian host parents use

412   multiple visual cues in rejecting parasitic eggs. Proceedings of the National Academy

413   of Sciences USA 107: 8672-8676.

414   Spottiswoode CN, Stevens M 2012. Host-parasite arms races and rapid changes in bird egg

415   appearance. American Naturalist 179: 633-648.

416   Stevens M, Troscianko J, Spottiswoode CN 2013a. Repeated targeting of the same hosts by a

417   brood parasite compromises host egg rejection. Nature Communications 4: 2475.

418   Stevens M, Marshall KLA, Troscianko J, Finlay S, Burnand D, Chadwick SL 2013b. Revealed by

419   conspicuousness: distractive markings reduce camouflage. Behavioral Ecology. 24:

420   213-222.

421   Stoddard MC, Prum RO 2011. How colorful are birds? Evolution of the avian plumage color

422   gamut. Behavioral Ecology 22: 1042-1052.

423   Stoddard MC, Stevens M 2011. Avian vision and the evolution of egg color mimicry in the

424   common cuckoo. Evolution 65: 2004-2013.

425   Taborsky M 2014. Tribute to Tinbergen: The four problems of biology. A critical appraisal.

426   Ethology 120: 224–227.

427   Tibbetts EA 2002. Visual signals of individual identity in the paper wasp *Polistes fuscatus*.

428   Proceedings of the Royal Society London B 269: 1423-1428.

429   Tinbergen N 1951. The study of instinct. Oxford University Press, New York.

430   Tinbergen N, Broekkhuysen GJ, Feekes F, Houghton JCW, Kruuk H, Szulc E 1962. Eggshell

431   removal by the Black-headed Gull, *Larus ridibundus* L.: a behaviour component of

432   camouflage. Behaviour 19: 74-117.

433   Tinbergen N 1963. On aims and methods of ethology. Zeitschrift für Tierpsychologie 20: 410-

434   433.

435   Weidinger K 2001. Does egg colour affect predation rate on open passerine nests?

436   Behavioral Ecology and Sociobiology 49: 456-464.