

# Evolutionary Ecology

## Explaining variation in brood parasitism rates between potential host species with similar habitat requirements

--Manuscript Draft--

<b>Manuscript Number:</b>	EVEC-D-15-00179R1	
<b>Full Title:</b>	Explaining variation in brood parasitism rates between potential host species with similar habitat requirements	
<b>Article Type:</b>	Original Research	
<b>Keywords:</b>	brood parasitism; common cuckoo; egg rejection; host specificity; nest defence; Oriental reed warbler; parasitism rate; reed parrotbill; Yellow river delta.	
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<b>Funding Information:</b>	the National Natural Science Foundation of China (31301888)	Dr. Donglai Li
	the National Natural Science Foundation of China (31272328 and 31472013)	Dr. Wei Liang
	Open Fund of Ministry of Education Key Laboratory for Biodiversity Sciences and Ecological Engineering, Beijing Normal University (K1401)	Dr. Donglai Li
	General scientific research project of Education Department of Liaoning Province (L2015196)	Dr. Donglai Li
	National Basic Research Program of China (2006CB403305)	Prof. Zhengwang Zhang
	United Foundation for Natural Science of National Natural Science Foundation of China and People's Government of Guangdong Province (U0833005)	Prof. Zhengwang Zhang
	the Research Council of Norway (218144)	Dr. Bård G. Stokke
	Human Frontier Science Program (awards RGY69/2007 and RGY83/2012)	Prof. Tomáš Grim

	the Czech Science Foundation (grant no. P506/12/2404)	Prof. Tomáš Grim
<b>Abstract:</b>	<p>Host specialization evolved in many parasite-host systems. Evolution and maintenance of host specificity may be influenced by host life-history traits, active host selection by the parasite, and host anti-parasite strategies. The relative importance of these factors is poorly understood in situations that offer parasites a choice between hosts with similar habitat requirements. The common cuckoo <i>Cuculus canorus</i> is a generalist parasite on the species level, but individual females prefer particular host species. In reed beds of the Yellow River delta, China, two potential hosts with similar nest characteristics, Oriental reed warblers <i>Acrocephalus orientalis</i> and reed parrotbills <i>Paradoxornis heudei</i>, breed in sympatry. We found that warblers were parasitized at much higher rates than parrotbills. Both hosts recognized and rejected non-mimetic model eggs well, indicating that they have been involved in an arms-race with cuckoos. Cuckoo eggs closely resembled warbler eggs, and such eggs were mostly accepted by warblers but rejected by parrotbills. Only warblers recognized adult cuckoos as a specific threat. Both hosts were equally good at raising cuckoo chicks. Low nest density, partial isolation by breeding time, small scale differences in nest and nest site characteristics, and high rejection rates of natural cuckoo eggs are likely responsible for the low current parasitism rate in parrotbills. This study emphasizes the importance of integrating the study of general host life-history characteristics and specific anti-parasitism strategies of hosts across all breeding stages to understand the evolution of host specificity.</p>	
<b>Response to Reviewers:</b>	Please see attached file as "Reply to comments (EVEC-D-15-00179)_R1".	

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1 **Explaining variation in brood parasitism rates between potential host species**  
2 **with similar habitat requirements**

3

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18

19 **Word count:** 91889693

20

21 **Running title:** Cuckoo host selection

22

23 **Abstract**

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25 maintenance of host specificity may be influenced by host life-history traits, active  
26 host selection by the parasite, and host anti-parasite strategies. The relative  
27 importance of these factors is poorly understood in situations that offer parasites a  
28 choice between hosts with similar habitat requirements. The common cuckoo *Cuculus*  
29 *canorus* is a generalist parasite on the species level, but individual females prefer  
30 particular host species. In reed beds of the Yellow River delta, China, two potential  
31 hosts with similar nest characteristics, Oriental reed warblers *Acrocephalus orientalis*  
32 and reed parrotbills *Paradoxornis heudei*, breed in sympatry. We found that warblers  
33 were parasitized at much higher rates than parrotbills. Both hosts ~~well~~-recognized and  
34 rejected non-mimetic model eggs well, indicating that they have been involved in an  
35 arms-race with cuckoos. Cuckoo eggs closely resembled warbler eggs, and such eggs  
36 were mostly accepted by warblers but rejected by parrotbills. Only warblers  
37 recognized adult cuckoos as a specific threat. Both hosts were equally good at raising  
38 cuckoo chicks. ~~This is in line with the hypothesis that an effective anti-parasitism~~  
39 ~~defence will lower the selection pressure on defences at later stages.~~ Low nest density,  
40 partial isolation by breeding time, small scale differences in nest and nest site  
41 characteristics, and high rejection rates of natural cuckoo eggs are likely responsible  
42 for the low current parasitism rate in parrotbills. This study emphasizes the  
43 importance of integrating the study of general host life-history characteristics and

44 specific anti-parasitism strategies of hosts across all breeding stages to understand the  
45 evolution of host specificity.

46

47 **Keywords:** brood parasitism; common cuckoo; egg rejection; host specificity; nest  
48 defence; Oriental reed warbler; parasitism rate; reed parrotbill; Yellow river delta.

49

50 **Introduction**

51 Generalist parasites often form specialized races, each adapted to a particular host via  
52 highly polygenic morphological and physiological traits (Futuyma and Moreno 1988),  
53 yet still belonging to a single species (i.e., host races may be connected by gene flow).  
54 For example, the common cuckoo, *Cuculus canorus* (hereafter cuckoo), exploits the  
55 parental care of many smaller passerines across Eurasia (Moksnes and Røskaft 1995).  
56 The cuckoo is a generalist at the species level, but individual cuckoo females prefer  
57 one or a few host species (Gibbs et al. 2000; Fossøy et al. 2011). Cuckoos have  
58 evolved distinct egg morphs that mimic particular host species in colour, spottiness,  
59 and size (Moksnes and Røskaft 1995) to reduce the risk of host egg rejection (Brooke  
60 and Davies 1988).

61 Despite intense research, especially during recent decades, the mechanisms  
62 underlying host selection in cuckoos remain poorly known. This is because there are  
63 many factors that may contribute to host selection (Soler et al. 1999), making it  
64 difficult to investigate their relative importance. Some, like foreign egg rejection, may  
65 represent specific anti-parasite adaptations (Davies ~~and~~ Brooke 1989; Moksnes et al.  
66 1991a) while others, like nest design ([Grim et al. 2009](#)) or chick diet ([Yang et al.](#)  
67 [2013](#)), probably did not evolve in response to parasitism (~~Grim et al. 2001~~). A strong  
68 test to understand causes of host selection is to analyse parasitism in sympatrically  
69 occurring potential hosts with similar nest characteristics, food and habitat  
70 requirements. This ~~was done~~ has rarely [been done](#) so far ([Ortega and Cruz 1991](#); [Peer](#)  
71 [and Bollinger 1997](#); Mermoz and Fernández 1999; Edvardsen et al. 2001; Grim et al.  
72 2011).

73 In the reed beds of the Yellow River Delta, China (YRD), two potential cuckoo  
74 hosts breed in sympatry: the Oriental reed warbler, *Acrocephalus orientalis*, and the  
75 reed parrotbill, *Paradoxornis heudei* (hereafter, warbler and parrotbill, respectively).  
76 The two species are phylogenetically distant, but they construct nests that are  
77 surprisingly similar in appearance and position (Fig. 1). Previous work, however,  
78 showed that warblers are commonly victimized by cuckoos in YRD and elsewhere in  
79 Eastern China, whereas parrotbills are almost never parasitized (Yang et al. 2014).  
80 These differences are striking considering the extremely homogeneous habitat (reed  
81 beds) that both passerines share. Disentangling reasons for such patterns requires a  
82 comprehensive approach that considers all potential factors, including nest site  
83 locations (Moskát and Honza 2002) and host responses to parasites at all stages of  
84 development, i.e. [adults \(Sealy et al. 1998\)](#), [eggs \(Davies and Brooke 1989\)](#), [and](#)  
85 [chicks ~~and adults~~ \(Grim et al. 2011, 2006a\)](#). Therefore we combined these approaches  
86 and studied both general life-history traits and potentially specific anti-parasite host  
87 responses at adult, egg, and chick stages in order to comprehensively understand host  
88 selection in a homogeneous ecological setting ([see also Grim et al. 2011](#)).

89

## 90 **Materials and Methods**

91 We carried out the fieldwork from May to August in 2008 (parrotbills only) and in  
92 2010–2012 (warblers and parrotbills) in the YRD National Nature Reserve  
93 (37°35′–38°12′ N, 118°33′–119°20′ E), Shandong, Eastern China. The study area is  
94 located in the second largest estuarine wetland area of China and contains extensive

95 reed habitats, interspersed with stretches of black locust *Robinia pseudoacacia* forests  
96 and farmlands (see Li et al. 2015a for more details). Warblers are recognized as the  
97 main hosts of the cuckoo in lowland reed habitats of Eastern Asia (Yang et al. 2012,  
98 2014). Parrotbills are potential cuckoo hosts, but reports of parasitism are very rare  
99 (Lin et al 2008; Yang et al. 2012, 2014). Although a larger area was searched for nests  
100 (see below), most nests were found in three specific reed bed plots (Fig. S1). We  
101 systematically searched for nests of the two passerines ~~during throughout~~ the breeding  
102 season. Most nests (80.0%, n = 526) were found when they were at the nest building  
103 or egg stage and we randomly selected nests for experiments. All nests, experimental  
104 or not, were monitored every 1-4 days until the final nest fate was determined.

105 Our focal~~us~~ host species (~~one+~~ warbler and ~~one+~~ parrotbill) is an ideal study  
106 system - simple and tractable (cf. multiple hosts in other habitats making such systems  
107 less tractable, see also discussion in Grim et al. (2011)). ~~Therefore, comparing two~~  
108 ~~species in this particular case is not pseudoreplication—the two potential hosts system~~  
109 ~~is simply a full reality to test the host choice, see also discussion in Grim et al. (2011).~~

110 Cuckoo parasitism rate was defined as a proportion of active nests that we found  
111 parasitized. Parasitism rates in any hosts may potentially be underestimated due to the  
112 high egg rejection rates by hosts (Davies 2000). However, we find this possibility  
113 unlikely for the following reasons. First, among parrotbill nests that were visited daily  
114 during the egg-laying stage, we only found one case of a missing host egg (n = 32).

115 Second, cuckoos typically remove one or several eggs from each host nest during the  
116 act of parasitism (Moksnes et al. 2000). Non-parasitized parrotbills usually have a



117 clutch size of 5 eggs (83.1%, n = 83), and there was no significant difference in the  
118 percentage of nests with less than 5 eggs before (17.9%, n = 46) and after (23.3%, n =  
119 37) cuckoo parasitism commenced in the area (Chi-square test:  $\chi^2 = 0.02$ , df = 1,  $p =$   
120 0.88). This suggests that at most only a few parasitized parrotbill nests escaped our  
121 attention.

122 The local abundance and distribution of each species was comprehensively  
123 surveyed along the roads or paths that pass through almost all reed habitats at the  
124 study site. One survey was conducted every year when most territories were  
125 established, in the first week of June. All three study species were easily visible due to  
126 their conspicuous behaviour. Territories were marked using a GPS (Garmin 60s), from  
127 which local population sizes were estimated. The spatial breeding distribution of each  
128 bird species was measured on GoodyGIS (Version. 3.21; <http://www.goodygis.com/>)  
129 based on the GPS data. The nest density of each host species was calculated as the  
130 total number of nests divided by the breeding area per year (see, e.g., Samaš et al.  
131 2013, see also Jelínek et al. 2014). ~~which should~~ This estimate constitutes a suitable  
132 index for comparing the relative breeding population for each host species because  
133 both parrotbill and warbler nests were searched with similar search effort. Importantly,  
134 the method directly takes into account all simultaneously active nests that are  
135 available to cuckoos in the peak part of the season.

136 We investigated differences in characteristics of nests and nest sites between  
137 parrotbills and warblers, following the protocol of Moskát and Honza (2000): (1)  
138 distance from nest to the closest potential cuckoo perch site, i.e. tree or electric wire

139 (to the nearest m); (2) distance to the closest reed edge (m); (3) nest visibility to a  
140 human observer (DL), on ordinal scale of five degrees from bad to good visibility; (4)  
141 the height of the reeds above the nest (m); (5) the number of green reed stems in a 0.5  
142 × 0.5 m quadrat at breast height (1.5 m) around the nest; (6) the mean height of the  
143 five highest reed stems in a 0.5 × 0.5 m quadrat of the nest site (m); not used by  
144 Moskát and Honza (2000); (7) the nest height above the water or ground (m); (8) the  
145 nest volume, an index expressing the size of the nest, which was calculated by  
146 multiplying three values: (a) outer nest height from the bottom of the nest to the rim;  
147 (b) maximum outer nest width; and (c), minimum outer nest width (all to the nearest  
148 cm).

149 In order to investigate specific host responses to adult parasites, we presented  
150 stuffed dummies near host nests, following the protocol of [Sealy et al. \(1998\)](#) and  
151 Campobello and Sealy (2010). Dummies of three species were used (two specimens  
152 per each to minimize the risk that differences between treatments would be a  
153 by-product of a particular specimen, see Trnka and Grim 2013), representing a brood  
154 parasite (common cuckoo, gray morph), a predator of adults (sparrowhawk *Accipiter*  
155 *nisus*), and non-threatening species as a control (spotted dove *Spilopelia chinensis*). A  
156 randomly chosen specimen was placed on bamboo sticks postured in typical life-like  
157 position about 0.5 m from the focal nest and at the same height as the nest rim with  
158 the head facing the rim.

159 The responses of nest owners were observed from a distance of about 10-20 m  
160 from a hide. Behaviour was also video-recorded by a camera placed 1-2 m from the

161 nest. Generally, the nest owners would return within 2-3 mins, and the responses were  
162 recorded for 5 min from the return of the first bird. Each nest was tested with all three  
163 ~~specimens-dummies~~ presented in a random order and separated by 30 mins. Nests  
164 were randomly selected during the egg-laying or early incubation stage ( $\leq 6$   
165 incubation days). ~~The response of the H-host responses to the specimen-were~~as rated  
166 on a four-step scale following Moksnes et al. (1991**b**): (1) No reaction, in which the  
167 hosts paid no attention to the ~~specimendummy~~, and in some cases, the host even sat  
168 on the nest directly; (2) Distress calling, in which the host uttered distress and alarm  
169 calls but was not willing to approach the ~~specimendummy~~; (3) Mobbing, in which the  
170 host approached the ~~specimen-dummy~~ with aggressive postures and alarm calls, but  
171 never made physical contact; (4) Attacks, in which the host vigorously attacked (i.e.,  
172 contacted) the dummy. The aggressive response was combined into two categories: no  
173 aggression (1 and 2) and aggression (3 and 4) for statistical analysis (Røskaft et al.  
174 2002, Grim et al. 2011). ~~In cases when most individuals respond aggressively but~~  
175 ~~some respond with few attacks whereas others respond with many attacks, ordinal or~~  
176 ~~nominal behavioural scales may lack power to detect existing and biologically~~  
177 ~~relevant effects (see analyses in Trnka et al. 2012). Therefore, For a separate analysis~~  
178 ~~(see below)~~ we ~~additionally~~ recorded the exact number of contact body attacks during  
179 5 min based on the video recordings ~~(for a separate analysis, see below)~~.

180 Variation in appearance between the eggs of cuckoos and those of the two  
181 potential host species was measured by spectrophotometry. Egg reflectance spectra  
182 (300–700 nm; 0.597-nm intervals) of three randomly selected portions of the

183 background, a light spot, and a dark spot on each egg were measured using a  
184 miniature fibre optic spectrometer (AVANTES) connected to a portable computer. All  
185 measurements were taken at a 45° angle and cover an area of approximately 1 mm<sup>2</sup>.  
186 In total, 792 spectra readings were collected from 55, 19, and 14 eggs of warblers,  
187 cuckoos, and parrotbills, respectively.

188 We artificially parasitized nests with one of three egg types: real cuckoo eggs,  
189 blue model eggs, and conspecific eggs. We used natural cuckoo eggs to directly  
190 quantify selection pressure by hosts to natural parasitism; some naturally laid (i.e.  
191 non-experimental) parasite eggs may be rejected by hosts before researchers notice  
192 them (but see above), therefore an experimental approach is needed to avoid biases in  
193 estimates of egg rejection rates (Moksnes and Røskaft 1992, Samas et al. 2014). We  
194 employed non-mimetic blue models as a standardized stimulus, which was identical  
195 for both study host species (see also Grim et al. 2011). Conspecific eggs were used  
196 because rejection of both real cuckoo eggs and non-mimetic models may represent a  
197 by-product of host egg rejection abilities evolved due to conspecific parasitism  
198 (Samas et al. 2014, [Liang et al. 2016](#)).

199 Real cuckoo eggs were transferred from parasitized warbler nests into  
200 non-parasitized warbler and parrotbill nests. In six cases, warbler eggs were used  
201 instead of cuckoo eggs as the experimental eggs in the experiments with reed  
202 parrotbills, because of scarcity of cuckoo eggs and due to that warbler eggs are very  
203 similar to cuckoo eggs in appearance (see results). Indeed, there was no **variation**  
204 **difference** in parrotbill rejection of cuckoo (76.9%, n = 12) and warbler eggs (83.3%,

205 n = 6; Fisher Exact Test:  $p = 1.00$ ). The data from the two groups were therefore  
206 merged.

207 The blue model eggs were made of synthetic clay. The mass of these eggs ( $3.14$   
208  $\pm 0.04$  g;  $n = 46$ ) were similar to those of real cuckoo eggs ( $3.13 \pm 0.20$  g,  $n = 38$ ;  $t =$   
209  $0.40$ ,  $df = 82$ ,  $p = 0.69$ ), but the egg sizes (egg length:  $19.44 \pm 0.76$  mm; egg breadth:  
210  $15.42 \pm 0.41$  mm;  $n = 46$ ) were slightly smaller than real cuckoo eggs (egg length:  
211  $22.02 \pm 0.90$  mm; egg breadth:  $16.26 \pm 0.42$  mm;  $n = 38$ ; all  $p < 0.0001$ ). Finally, we  
212 included a control group, i.e. nests whose content was not manipulated<sup>d</sup> but was  
213 monitored to estimate the baseline nest desertion rates (Samas et al. 2014).

214 Host nests were monitored daily or every second day for six consecutive days  
215 after the initial placement of the eggs, following the standard criteria for rejection  
216 (Moksnes et al. 1991<sup>a, b</sup>). Responses were defined as (1) ejection: the parasitic egg  
217 disappeared or were still incubated but heavily pecked (model eggs); (2) desertion: the  
218 nest was abandoned with or without any damage to either the parasitic egg or the  
219 hosts' own eggs; and (3) acceptance: the clutch with the parasitic egg was still warm  
220 without peck-broken egg(s) and was incubated at the end of the monitoring period.  
221 Nests that were depredated within the 6-day period were excluded from analyses.  
222 Desertions were included as a rejection response because no control nests were  
223 deserted (Results).

224 We carried out cross-fostering experiments in order to investigate whether  
225 warblers and parrotbills differed in their ability to raise a cuckoo chick. We exchanged  
226 14 cuckoo chicks (aged 3–5 days) from naturally parasitized warbler nests with host

227 chicks in non-parasitized parrotbill (n = 6) or warbler (n = 8) nests. Another 18  
228 cuckoo chicks in naturally parasitized nests served as the control group. We  
229 cross-fostered cuckoos between naturally parasitized and non-parasitized nests to  
230 check whether cross-fostering of cuckoos from warbler to parrotbill nests itself did  
231 not affect their growth and survival in parrotbill nests (see also Grim 2007). All the  
232 cuckoo chicks were monitored every other day until fledging or death. Body weight  
233 (0.01 g) and tarsus length (mm) were measured daily or every other day until  
234 fledging.

235

### 236 **Statistical analyses**

237 The date of the first egg laid in each focal nest was either recorded directly (for nests  
238 found in nest building and egg-laying stage) or inferred (nests found with completed  
239 clutches or chicks) using incubation time of 14 and 12 days for two hosts and cuckoo  
240 respectively, and fledging time of 14 and 20 days for two hosts and cuckoo,  
241 respectively (D. Li et al. unpublished data). We used the first egg-laying date (or egg  
242 laying for the cuckoo) for each nest to compare breeding time synchronization for the  
243 cuckoo and two hosts. Independent sample t-tests were used to compare the breeding  
244 time among groups because all data fitted normality distribution.

245 All egg and nest characteristics were assessed for normality using the  
246 Shapiro–Wilk tests. When necessary, data were ln transformed to achieve normality.  
247 In cases where there was still a lack of normality after transformation, we used  
248 Mann-Whitney U tests to compare the differences between groups, otherwise an

249 independent sample t-tests were used. The sample size for nest sites and nest  
250 characteristics varied for different comparisons because weather or predators  
251 destroyed some nests. For analyses of differences in parasitism rates, egg rejection  
252 rates and fledgling success rates, Pearson's  $\chi^2$  tests were used with Yates' continuity  
253 correction, except when 20% of the expected values in the contingency table were  $<5$ ,  
254 in which case we used Fisher exact tests.

255 We used the generalized linear mixed model (GLMM) to test the host responses  
256 to dummies with response variable as nominal (no aggression or aggression) or  
257 continuous (number of contact attacks per 5 min). All GLMMs included two main  
258 fixed factors: host species (nominal) and dummy species (nominal) and their  
259 interaction. Other potential confounding factors, namely, year and nest stage (two  
260 categories: egg-laying vs. early incubation-, i.e. less than 6 days of incubation) were  
261 also statistically controlled for. Specimen id was modelled as a fixed (rather than a  
262 random) effect because the number of levels was lower than six (see Fox et al. 2015).

263 Nest identity was entered as a random factor to control for non-independence among  
264 trials at the same nest. The first GLMM used a binomial distribution with a logit link,  
265 as the host aggression is a binary response (no aggression or aggression). The second  
266 GLMM used a Poisson distribution with a log link, because the response variable  
267 “number of attacks” is a count of occurrences during a fixed period of time. We  
268 followed backward elimination of non-significant terms. We checked the final  
269 (minimum adequate) model by adding the previously removed terms (one at a time)  
270 and found that none explained any significant variation. Test statistics and *P*-values

271 reported are from a sequential backward elimination procedure just before the  
272 particular term (being the least significant) and was removed from the model. The  
273 minimum adequate model contained only significant predictors.

274 Three separate principal component analyses were used to explore the colour  
275 variations in the background and the two types of spots for the three species. This type  
276 of analysis is useful for evaluating variation in spectral data because it reduce the  
277 correlated variables of reflectance spectra into a few orthogonal variables that  
278 describe achromatic (brightness) and chromatic (colour) variation (Cuthill et al. 1999,  
279 Cherry and Bennett 2001). The first principal component (PC1) represents variation in  
280 mean reflectance, or brightness, whereas the subsequent principal components  
281 represent variation in colour (Endler and They 1996). PC1 explaineds 83.6%, 85.5%,  
282 and 71.0% of the overall colour variations of background, light spots, and dark spots,  
283 respectively, whereas the PC2 and PC3 explaineds the remaining variation among  
284 8.4–13.9% and 3.3–6.2% respectively. The coefficients were plotted against  
285 wavelength to depict the variation in colour that was explained by each principal  
286 component (Fig. S2), and the differences in principal component scores between  
287 cuckoo eggs and those of the two hosts were compared to reflect the egg mimicry.

288 ~~Following the suggestion in Grim (2006), w~~We used logistic regression tTo  
289 estimate standard growth parameters ( $K$  = growth rate,  $A$  = asymptotic mass) of  
290 cuckoo chicks ~~we used logistic regression~~-(for details see Grim 2006**b**). Only chicks  
291 with growth data across the majority of nestling period could be used to estimate  
292 standard growth parameters (Starck and Ricklefs 1998, Grim 2006**b**). The benefit of



293 this approach is to estimate K and A parameters at individual chick level that can be  
294 included in future meta-analyses. The disadvantage is that, chicks that died, due to  
295 predation or inclement weather, before reaching the asymptotic phase of growth had  
296 to be excluded. ~~Therefore, w~~We run a separate analysis based on all growth data, with  
297 chick id as a random effect; the single population estimates of K and A were very  
298 similar to those ~~reported here~~based on individual chicks (Table 3).

299 ~~We used O~~one-way ANOVAs ~~were used~~ to compare the estimated growth  
300 parameters (K, A) of young cuckoo raised in three groups (Kruskal-Wallis tests on the  
301 same data lead to same conclusions, results not shown). ~~Only chicks with growth data~~  
302 ~~across the majority of nestling period could be used to estimate standard growth~~  
303 ~~parameters (Starck and Ricklefs 1998, Grim 2006). The benefit of this approach is to~~  
304 ~~estimate K a A parameters at individual chick level that can be included in future~~  
305 ~~meta-analyses. The disadvantage is that, chicks that died, due to predation or~~  
306 ~~inclement weather, before reaching the asymptotic phase of growth had to be~~  
307 ~~excluded. We run a separate analysis based on all growth data, with chick id as a~~  
308 ~~random effect; the single population estimate of K and A were very similar to those~~  
309 ~~reported here (Table S2).~~ The differences in fledging age and body measures (body  
310 mass and tarsus length) were only compared between host species (naturally  
311 parasitized warblers and cross-fostered warblers were pooled because of the relatively  
312 small sample sizes) using independent sample t-tests.

313 All statistical analyses were carried out using IBM SPSS 20.0. The statistical  
314 tests were two-tailed, and ~~data was~~estimates are reported as means  $\pm$  SE, ~~exce~~cept

315 when stated otherwise. Significance levels were set at  $p < 0.05$ .

316 In the present study, blinded methods were not used. It was not possible to record  
317 data blindly because our study involved focal animals in the field.

318

## 319 **Results**

### 320 *Parasitism rate*

321 The overall parasitism rate in warblers (24.9%;  $n = 362$ ) was significantly higher than  
322 in parrotbills (0.8%;  $n = 132$ ; Chi-square test:  $\chi^2 = 35.81$ ,  $df = 1$ ,  $p < 0.001$ ; Table S1).

323 There was no significant annual variation in the parasitism rate in the two hosts  
324 (warbler:  $\chi^2 = 0.44$ ,  $df = 2$ ,  $p = 0.80$ ; parrotbill:  $\chi^2 = 2.32$ ,  $df = 3$ ,  $p = 0.51$ ).

325 Approximately 2.5% of the warbler nests ( $n = 362$ ) were multiply parasitized  
326 (contained two cuckoo eggs), and there was no annual variation in multiple parasitism  
327 ( $\chi^2 = 0.02$ ,  $df = 2$ ,  $p = 0.99$ , Table S1).

328

### 329 *Spatial distribution, nest density, nest and nest site characteristics*

330 Our survey disclosed that parrotbills have a considerably larger spatial breeding  
331 distribution (ca. 103 km<sup>2</sup>) than warblers (ca. 3.67 km<sup>2</sup>) in the Yellow River delta, but  
332 the estimated average nest density (11.0 nests/km<sup>2</sup>) of parrotbills was only about a  
333 ~~quarter~~ of that of warblers (40.8 nests/km<sup>2</sup>) from the data collected in three  
334 main study sites (Fig. S1 and Table S2). Warblers ~~were mainly found~~ concentrated in  
335 three main reed plots (>90% of the population in the study area), where they breed in  
336 the densest and tallest reeds, ~~but~~ the breeding populations showed dramatic annual

337 fluctuations in each reed plots (Table S2) depending on the local hydrological  
338 conditions for reed growth. Parrotbills breed in a broader range of reeds, but the nest  
339 density was not uniform: parrotbill nest density in site A was much higher than in site  
340 B and C (Table S2). Within the three study plots, the nest density of parrotbills was  
341 much lower than that of warblers in site B and C, but was about half (0.58) of that of  
342 warblers in site A (Table S2).

343 Both parrotbills and warblers built cup nests of remarkably similar appearance  
344 sewn around 3-7 reed stems (Fig. 1). There were no significant differences between  
345 the distances of parrotbill and warbler nests to cuckoo perches, but parasitized warbler  
346 nests were closer to perches than non-parasitized ones (Table 1). There were no other  
347 nest or nest-site characteristics showing any statistically significant difference  
348 between parasitized and non-parasitized warbler nests. However, compared to  
349 parrotbills, warblers generally placed their nests further from the nearest reed edge  
350 (from water or dry land, but significantly so only for warblers that were not  
351 parasitized), in larger and denser reeds, nested in less dry reeds, had larger and more  
352 visible nests, and placed their nests higher in the reeds, ~~but the warblers that were~~  
353 ~~parasitized were more like to place their nests further from the nearest reed edge than~~  
354 ~~parrotbills~~ (Table 1).

355

### 356 *Timing of breeding season*

357 Parrotbills were local residents and started to breed earlier (first egg-laying dates for  
358 the first nest in each season: 2008: April 28; 2010: May 15; 2011: May 8; 2012: April

359 25) than migratory warblers (2010: May 25; 20110: May 25; 2012: May 18) or  
360 migratory cuckoos (2010: June 1; 2011: June 6; 2012: May 30). There were no  
361 significant differences between the averages ~~of the~~ first egg-laying dates of cuckoos  
362 and warblers during 2010–2011 (2010:  $t = 1.13$ ,  $df = 176$ ,  $p = 0.26$ ; 2011:  $t = 0.27$ ,  $df$   
363  $= 138$ ,  $p = 0.79$ ), but in 2012, cuckoos initiated their egg-laying season somewhat  
364 later than warblers ( $t = 2.57$ ,  $df = 150$ ,  $p = 0.01$ ). The average first egg-laying dates of  
365 parrotbills were much earlier than those of cuckoos (for all years,  $p \leq 0.005$ ) and  
366 warblers (for all years,  $p \leq 0.005$ ) during the three years of study. In fact, on  
367 average, 55.3% (2010: 38.5%,  $n = 26$ ; 2011: 69.4%,  $n = 36$ ; 2012: 53.7%,  $n = 41$ )  
368 parrotbill nests were fully laid and the eggs were nearly ready to hatch before the  
369 onset of cuckoo parasitism. However, still a considerable number of parrotbill nests ( $n$   
370  $= 46$ ) were available to cuckoos, but very few actually were used (Table S1).  
371 Considering the time when only the parrotbill nests available to cuckoos during  
372 2010-2012, parasitism rate in parrotbills (0%,  $n = 46$ ) was also significantly lower  
373 than in warblers (25.9%;  $n = 348$ ;  $\chi^2 = 13.99$ ,  $df = 1$ ,  $p < 0.001$ ).

374

#### 375 *Response to dummies*

376 Ordinal scoring showed that warblers were more aggressive (68% of trials) than  
377 parrotbills (19% of trials;  $F_{1,209} = 24.18$ ,  $p < 0.0001$ ; Fig.2a). Both specimen id ( $F_{2,204}$   
378  $= 0.15$ ,  $p = 0.86$ ), specimen-host species interaction ( $F_{4,205} = 1.18$ ,  $p = 0.32$ ) and  
379 breeding stage ( $F_{1,204} = 0.35$ ,  $p = 0.56$ ) were non-significant and removed from the  
380 final model. The final model controlled for significant differences among years ( $F_{2,209}$

381 = 3.78,  $p = 0.024$ ) and nests ( $Z = 3.09$ ;  $p = 0.002$ ).

382 Warblers launched a larger number of direct attacks (estimate  $\pm$  SE:  $6.83 \pm 2.12$ )  
383 to all dummies than parrotbills ( $0.08 \pm 0.04$ ,  $F_{2,207} = 45.59$ ,  $p < 0.0001$ ), and were  
384 especially aggressive against the cuckoo when compared to the aggression of the  
385 parrotbill ( $14.61 \pm 4.53$  vs  $0.07 \pm 0.05$ ;  $t = 5.32$ ,  $p < 0.0001$ ). Both years ( $F_{2, 205} = 2.62$ ,  
386  $p = 0.08$ ) and breeding stage ( $F_{1, 204} = 0.11$ ,  $p = 0.75$ ) were non-significant and  
387 removed from the final model. The final model controlled for significant differences  
388 among nests ( $Z = 4.60$ ,  $p < 0.000$ ), specimens ( $F_{2,207} = 11.06$ ,  $p < 0.0001$ ), and ~~in~~ the  
389 interaction between host species and specimens ( $F_{2,207} = 14.20$ ,  $p < 0.0001$ ). The  
390 warblers showed more aggressive attacks towards mounted cuckoos than hawks and  
391 doves ( $F_{2, 207} = 5.14$ ,  $p = 0.007$ ; cuckoo versus hawk:  $t = 3.21$ ,  $df = 207$ ,  $p = 0.002$ ;  
392 cuckoo versus dove:  $t = 3.20$ ,  $df = 207$ ,  $p = 0.002$ ; Fig. 2b), whereas parrotbills  
393 showed no significant variation in the number of attacks they made towards cuckoos  
394 vs. the other two stuffed ~~specimens~~ dummy types ( $F_{2, 207} = 1.12$ ,  $p = 0.33$ ; cuckoo  
395 versus hawk:  $t = 1.00$ ,  $df = 207$ ,  $p = 0.32$ ; cuckoo versus dove:  $t = -1.24$ ,  $df = 207$ ,  $p$   
396 = 0.22; Fig. 2b).

397

### 398 *Egg mimicry*

399 Cuckoo egg background colour was pale green-blue, speckled and blotched with pale  
400 grey, light and olive green, and dark brown spots (Fig. 3b), displaying almost perfect  
401 mimicry of warbler eggs to the human eye and according to the objective spectral  
402 analysis. However, both the background colour and the light spots of the cuckoo eggs

403 were brighter than those of the warbler eggs (Fig. 3a). Parrotbill eggs were  
404 greenish-white with dark brown spots and blotches or clouds of underlying pale  
405 sienna spots (Fig. 1d; Fig. 3b), and varied considerably but differed distinctly from  
406 cuckoo eggs (Fig. 3b).

407 There were significant differences in three scores of PC1-3 between cuckoo and  
408 the two hosts (all  $p < 0.05$ ), except for the PC1 of the dark spots between cuckoo and  
409 warbler ( $t = 1.85$ ,  $df = 214$ ,  $p = 0.07$ ) and the PC2 of the background between cuckoo  
410 and warbler ( $t = 0.41$ ,  $df = 223$ ,  $p = 0.68$ ), and the PC3 of the dark spots between  
411 cuckoo and both hosts (cuckoo vs. warbler:  $t = 0.95$ ,  $df = 214$ ,  $p = 0.34$ ; cuckoo vs.  
412 parrotbill:  $t = -1.13$ ,  $df = 98$ ,  $p = 0.26$ ; Fig. S3).

413

#### 414 *Egg recognition experiments*

415 Neither parrotbills ( $n = 20$ ) nor warblers ( $n = 32$ ) in the control groups showed any  
416 egg rejection (rejection errors) or nest desertion (Fig. 4). Therefore, we included  
417 desertion as a specific response to parasitism.

418 Parrotbills (77.8%,  $n = 18$ ) displayed a higher rejection rate of real cuckoo eggs  
419 than did warblers (10.5%,  $n = 19$ ;  $\chi^2 = 14.40$ ,  $df = 1$ ,  $p < 0.001$ ; Fig. 4). Both hosts  
420 used ejection of the eggs from the nest as their only egg rejection strategy, with no  
421 loss sustained due to erroneous or accidental ejection of own eggs.

422 Parrotbills (78.9%,  $n = 19$ ) and warblers (75.8%,  $n = 33$ ) showed a similar high  
423 rate of egg rejection for non-mimetic blue model eggs ( $\chi^2 = 1.97$ ,  $df = 1$ ,  $p = 0.16$ ; Fig.

424 4). Ejection (both successful and attempted but unsuccessful) was the ~~—and in—~~ most

425 ~~eases ejection~~common method of rejection of the foreign eggs in both (parrotbills  
426 (93.3%, n = 15) ~~vs~~ and warblers (93.3% (n = 15) vs 92.0% (n = 25); Fisher exact  
427 test:  $p = 1.00$ ). However, while warblers successfully removed model eggs in most  
428 cases (91.3%, n = 23), parrotbills only successfully ejected 7.1% (n = 14) such eggs  
429 ( $\chi^2 = 22.20$ , df = 1,  $p < 0.001$ ). The inability of the parrotbills to eject model eggs  
430 always ended in either the forced acceptance of the parasite eggs (35.8%, n = 14) due  
431 to physical inability to reject the eggs or complete desertion (57.1%; n = 14) of the  
432 nest and breakage of almost all host own eggs (2–4 eggs). Two unsuccessful attempts  
433 to eject that finally led to nest desertion also contained two or three broken host eggs,  
434 but the rate of loss associated with damage to the host's own eggs was significantly  
435 lower for warblers (8.7%; n = 23) than parrotbills (71.4%, n = 14; Fisher exact test:  $p$   
436  $< 0.001$ ). Oriental reed warblers and reed parrotbills have distinctly different bill  
437 morphology (Xiong and Lu 2013). Due to their short and blunt bills, parrotbills are  
438 most probably not able to grasp eject eggs and therefore have to rely on puncture  
439 ejection (or desertion). This seemed to work without problems when ejecting real  
440 cuckoo eggs, but they obviously faced problems when trying to get rid of the  
441 thicker-shelled model eggs. Warblers, on the other hand, should be able to grasp eject  
442 eggs (Antonov et al. 2006), or puncture and remove even hard-shelled model eggs  
443 without any substantial costs (Honza and Moskat 2008). These results taken together  
444 strongly suggest that the “forced acceptance” of model eggs by parrotbills was  
445 simply due to their inability to remove such eggs (even though they were pecked, i.e.  
446 we observed pecking marks on the surface of the eggs).

447 Both parrotbills (12.0%, n = 25) and warblers (11.1%, n = 18) showed a low  
448 rejection rate of conspecific eggs which did not differ between the two hosts (Fisher  
449 Exact Test:  $p = 1.00$ ). The rejection by both species was by both ejection and  
450 desertion.

451

#### 452 *Cuckoo chick cross-fostering experiments*

453 There were no significant differences in the fledging success of cuckoo chicks among  
454 the three treatment groups (Table 2;  $\chi^2 = 2.57$ ,  $df = 2$ ,  $p = 0.28$ ). The parrotbill hosts  
455 did not discriminate against cuckoo chicks – there were no differences in the growth  
456 parameters of the cuckoo chicks raised in the original warbler nests, cross-fostered to  
457 different warbler nests and cross-fostered to parrotbill nests (Fig. 5, Fig. S4, Table 3).  
458 Furthermore, there was no significant variation in the fledging age (warbler:  $18.3 \pm$   
459  $0.3$  days, parrotbill:  $17.5 \pm 0.5$  days;  $t = -0.95$ ,  $df = 8$ ,  $p = 0.37$ ), fledging body mass  
460 (warbler:  $58.7 \pm 0.9$  g, parrotbill:  $56.4 \pm 2.6$  g;  $t = -1.04$ ,  $df = 8$ ,  $p = 0.33$ ) and  
461 fledging tarsus length (warbler:  $25.4 \pm 0.3$  mm, parrotbill:  $25.0 \pm 0.9$  mm;  $t = -0.51$ ,  
462  $df = 8$ ,  $p = 0.63$ ) of cuckoo chicks fostered by the two hosts.

463

#### 464 **Discussion**

465 Despite the very homogeneous habitat, cuckoos in the Yellow River delta parasitized  
466 warblers at much higher rates than parrotbills, and cuckoo eggs showed exquisite  
467 mimicry to warbler eggs, but not to parrotbill eggs. Hence, cuckoo parasitism was  
468 highly host-specific among these two sympatric reed bed breeding passerines, in line



469 with the host preference hypothesis (Moksnes and Røskaft 1995; Skjelseth et al.  
470 2004). This finding is intriguing, since our cross-fostering experiments showed that  
471 both hosts are equally good at raising cuckoo chicks.

472 Furthermore, egg recognition experiments disclosed that there were no significant  
473 differences in the egg recognition ability by warblers and parrotbills, as both show a  
474 high rejection rate of non-mimetic eggs. The highly developed ability to reject foreign  
475 eggs suggests that both warblers and parrotbills have been utilized by cuckoos in the  
476 past. However, cuckoos have only evolved mimetic eggs towards warblers.

477 The question then is why a cuckoo gens specializing on warblers has evolved,  
478 while at the same time there seems to be no gens utilizing parrotbills. Obviously, the  
479 fact that the parrotbill show high rejection rate of natural “warbler” cuckoo eggs  
480 appears to be an important factor in explaining the apparent low parasitism rate on  
481 parrotbills in our study area and elsewhere (Yang et al. 2014). The rejection of cuckoo  
482 eggs by this species has most likely evolved due to past parasitism by cuckoos and  
483 was not explained as a “collateral damage” (Samas et al. 2014) from adaptations  
484 against conspecific parasitism because (1) parrotbills rejected conspecific eggs rarely  
485 and at much lower rates than cuckoo eggs, and (2) we detected no cases of conspecific  
486 parasitism. However, cuckoos have not responded by evolving a mimetic egg. Hence,  
487 parrotbills are now difficult for cuckoos to successfully parasitize since their eggs are  
488 so different from the parrotbill eggs, even though we cannot rule out that they still are  
489 hosts in other parts of their breeding range. Could there be other characteristics of  
490 parrotbills that make them less likely to be favoured by cuckoos?

491

492 There were no significant differences in the general habitat patterns of the reed  
493 bed between the nest patches of the two hosts. In fact, the parrotbill territories often  
494 overlapped with the warbler territories. However, parrotbills preferred to nest in  
495 patches of reeds that were lower in height and with a greater percentage of dry reed  
496 stems than warblers (see also Li et al. 2015b). Hence, we cannot rule out host  
497 selection based on small scale differences between parrotbill and warbler nest and  
498 nest site characteristics (Moskát and Honza 2000; Antonov et al. 2007, i.e. the habitat  
499 imprinting hypothesis: (Teuschl et al. 1998)).

500 Host behaviour can also be influential for explaining variation in cuckoo  
501 parasitism (Gill et al. 1997; Davies 2000). The dummy experiments disclosed that  
502 warblers, but not parrotbills responded aggressively to cuckoos. Further, parrotbills, in  
503 contrast to warblers, did not recognize cuckoos as a specific threat. The response of  
504 warblers to the intruders was consistent with previous work on closely related great  
505 reed warblers *Acrocephalus arundinaceus* in Europe (Honza et al. 2006; Trnka and  
506 Grim 2013). Since warblers are noisy, aggressive and large birds, they are easy to  
507 detect. Parrotbills on the other hand are smaller and less conspicuous, and since they  
508 do not behave aggressively towards cuckoos, they are more difficult to detect (i.e.,  
509 lower opportunity for eavesdropping on these hosts by cuckoos).

510 Life-history features and adaptations by the hosts may contribute to host-specific  
511 parasitism (Antonov et al. 2010; Grim et al. 2011; Møller et al. 2011; Grim et al.  
512 2014). The parrotbill is a resident of the area and starts to breed much earlier than the

513 warbler and cuckoo, both of which are migratory, summer visitors. In fact, over half  
514 (52.7 %) the nests of parrotbills complete egg-laying before the cuckoo breeding  
515 season begins, thereby avoiding being parasitized by cuckoos, a fact that may likely  
516 contribute to the lower parasitism rate in reed parrotbills and lower selection on  
517 specific anti-cuckoo adaptations in this host (for similar cases see Peer and Bollinger  
518 1997; Gill 1998). However, in other areas, many resident birds are common hosts for  
519 cuckoos even though their breeding period is poorly synchronized with that of the  
520 cuckoo (Kim 1996; Medina and Langmore 2016). –Furthermore, although half of the  
521 nests of parrotbills in our study were available for parasitism, they still experienced a  
522 significantly lower parasitism rate than warblers. Therefore, our results suggest that  
523 being a resident and having a partially separated breeding season cannot solely  
524 explain the lower parasitism rate on parrotbills by cuckoos. Still, we cannot rule out  
525 that parrotbills have adopted an earlier initiation of breeding in order to decrease the  
526 risk of parasitism by cuckoos.

527 Warblers had a higher local density and aggregated breeding than parrotbills,  
528 which may make them more available and suitable as cuckoo hosts than parrotbills  
529 (Stokke et al. 2007; Soler et al. 2009; Jelínek et al. 2014). Hence, significantly less  
530 search effort is most likely required from cuckoos utilizing warblers than parrotbills.  
531 However, the apparent low parasitism rate of the parrotbills cannot be completely  
532 explained by differences in density, because it appears that the density of warblers and  
533 parrotbills were nearly similar in some areas (e.g. Area A, Fig S1), but still parasitism  
534 rates were strikingly different.

535 The mismatch in breeding synchrony between cuckoos and parrotbills (Møller et  
536 al. 2011) and the differences in aggression and nest/nest site characteristics may boost  
537 a possible “density” effect and lead to a low availability of parrotbills for parasitism.  
538 Hence, it seems likely that not only one but rather several mechanisms may additively  
539 and interactively to render parrotbills less suitable to cuckoos than warblers. It is  
540 important to acknowledge that our study is both restricted in time and space, making  
541 inference about the past and other sites impossible. Egg rejection in parrotbills may  
542 have evolved due to high parasitism in the past, perhaps in areas or times with higher  
543 density and a better breeding synchrony with cuckoos. Alternatively, rejection  
544 behaviour may be an ancestral trait that has been retained in the absence of parasitism  
545 even through evolutionary events on the species level (e.g. Rothstein 2001; Peer and  
546 Sealy 2004), or have evolved due to other reasons than brood parasitism (see Stokke  
547 et al. 2016 for a discussion of such events).

548

549 ~~Despite the very homogeneous habitat, cuckoos in the Yellow River delta parasitized~~  
550 ~~warblers at much higher rates than parrotbills (24.9% vs 0.8%), and cuckoo eggs~~  
551 ~~showed exquisite mimicry of warbler eggs, but not to the parrotbill eggs. Hence,~~  
552 ~~cuckoos showed host specific parasitism on among these two sympatric reed bed~~  
553 ~~breeding passerines, in this area, similar to results in Yang et al. (2014), in line with~~  
554 ~~the host preference hypothesis (Moksnes and Røskoft 1995; Skjelseth et al. 2004).~~  
555 ~~There were no significant differences in the general habitat patterns of the reed bed~~  
556 ~~between the nest patches of the two hosts. In fact, the parrotbill territories often~~

557 ~~overlapped the warbler territories. Although However, the parrotbills preferred to nest~~  
558 ~~in habitats patches of reeds that were lower in height and with a greater percentage of~~  
559 ~~dry reed stems than warblers (see also Li et al. 2015b), there were no significant~~  
560 ~~differences in the general habitat patterns of the reed bed between the nest patches of~~  
561 ~~the two hosts. In fact, the parrotbill territories often overlapped the warbler territories.~~  
562 ~~ThereforeHence, we cannot rule out host selection based on small scale differences~~  
563 ~~between parrotbill and warbler nest and nest site characteristics (Moskát and Honza~~  
564 ~~2000; Antonov et al. 2007, i.e. the habitat imprinting hypothesis (Teuschl et al. 1998))~~  
565 ~~cannot explain the significant difference in cuckoo parasitism between warblers and~~  
566 ~~parrotbills. Host behaviour can also be influential for explaining variation in cuckoo~~  
567 ~~parasitism (Gill et al. 1997; Davies 2000). The dummy experiments disclosed that~~  
568 ~~warblers, but not parrotbills responded aggressively to cuckoos. Further, parrotbills, in~~  
569 ~~contrast to warblers, did not recognize cuckoos as a specific threat. The response of~~  
570 ~~warblers to the intruders was consistent with previous work on closely related great~~  
571 ~~reed warblers *Acrocephalus arundinaceus* in Europe (Honza et al. 2006; Trnka and~~  
572 ~~Grim 2013). Since warblers are noisy, aggressive and large birds, they are easy to~~  
573 ~~detect. Parrotbills on the other hand are smaller and less conspicuous, and since they~~  
574 ~~do not behave aggressively towards cuckoos, they are more difficult for cuckoos to~~  
575 ~~detect (i.e., lower opportunity for eavesdropping on these hosts by cuckoos).~~

576 Life-history features and adaptations by the hosts may contribute to host-specific  
577 parasitism (Antonov et al. 2010; Grim et al. 2011; Møller et al. 2011; Grim et al.  
578 2014). The parrotbill is a resident of the area and starts to breed much earlier than the

579 warbler and cuckoo, both of which are migratory, summer visitors. In fact, over half  
580 (52.7 %) the nests of reed parrotbills complete egg laying before the cuckoo breeding  
581 season begins, thereby avoiding being parasitized by cuckoos, a fact that may be  
582 partly responsible for likely contribute to the lower parasitism rate in reed parrotbills  
583 (for a similar cases see Ortega and Cruz 1991; Peer and Bollinger 1997; Gill 1998).  
584 However, in other areas, many resident birds are common hosts for cuckoos , such as  
585 the Vinous throated parrotbill (*Paradoxornis webbianus*) in Korea, even though  
586 itstheir breeding timeperiod is poorly synchronized with that of the cuckoo (Kim 1996;  
587 Medina and Langmore 2016). Recent study in yellow-rumped thornbill, *Acanthiza*  
588 *chrysorrhoa*, also showed that even though this trornbill speices has shifted their  
589 breeding phenology by commencing the egg laying time earlier, they also heavily  
590 been parasitized by the shining bronze cuckoo, *Chalcites lucidus* (Medina and  
591 Langmore 2016). Furthermore, aAlthough half of the nests of parrotbills in our  
592 study were available for parasitism, they still experienced a significantly lower  
593 parasitism rate than warblers. Therefore, we concludeour results suggest that being a  
594 resident and having a partially separated breeding season were not sufficient tocannot  
595 solely explain the lower parasitism rate on parrotbills by cuckoos. HoweverStill, we  
596 cannot rule out that whether reed parrotbills have adopted an earlier initiation of  
597 breeding time in order to decrease the possibilityrisk of parasitism by cuckoos (Møller  
598 et al. 2011) is need further explored.

599 Previous study have showed that the host density have a good prediction for  
600 presence of cuckoo parasitism in one of its main host, reed warbler, in Europe (Stokke

601 et al. 2007). Even we didn't used the point count (or line transect) to estimate a kernel  
602 density of warblers and parrotbills, but used the nest density to assess the local density  
603 of these two hosts. We propose that tWarblers had ahe higher local density and  
604 aggregated breeding of warblersthan parrotbills, which may make them more suitable  
605 as cuckoo hosts than parrotbills (Stokke et al. 2007; Soler et al. 2009; Jelínek et al.  
606 2014). Hence, significantly less search effort is most likely required from cuckoos  
607 utilizing warblers than parrotbills. The mismatch in breeding synchrony between  
608 cuckoos and parrotbills may boost this effect (Møller et al. 2011) and lead to a low  
609 availability of parrotbills for parasitism. However, the apparent low parasitism rate of  
610 the parrotbills can'tcannot be completely explained by the density  
611 hypothesisdifferences in density, first because some host holding even low breeding  
612 density can be parasitized by cuckoo, second,because it appears that the density of  
613 each specieswarblers and parrotbills were nearly equalsimilar in some areas (e.g.Area  
614 A, Fig S1), but still parasitism rates were strikingly different,warbler and parrotbill  
615 the nest density of these two in Area A (Fig S1), yet parasitism rates are still very  
616 different.

617 Nest concealment and small nest entrances are well-known traits that prevent  
618 cuckoo parasitism on some potential hosts (Davies 2000). In a recent study of thrush  
619 species that use a cup shaped nest design, it was reported that the nest shape  
620 effectively prevented the cuckoo chicks from evicting the host eggs or chicks, thereby  
621 forcing cuckoo chicks to compete with host chicks, with fatal consequences for the  
622 parasite (Grim et al. 2011). In the present study, both reed parrotbills and Oriental

623 reed warblers build a similar cup nest utilizing 3–5 reed stems (Li et al. 2015), which  
624 appears to be very suitable for cuckoo parasitism. The volume of reed parrotbill nests  
625 was only about half of that of the Oriental reed warbler, but the nest volume is not the  
626 main constraint for cuckoo use, as many birds (e.g., vinous-throated parrotbill) that  
627 have even smaller nest volumes are parasitized by the common cuckoo. According to  
628 the perch proximity hypothesis, the distance of the nests to the closest perch site is an  
629 important factor that affects whether the nest can be parasitized by a cuckoo. In this  
630 study, the parasitized Oriental reed warbler nests were closer to the nearest perch than  
631 were the non-parasitized nests, but there was no significant difference between the  
632 average distances to the nearest perch of the two hosts' nests. None of the examined  
633 variables supported the nest exposure hypothesis that the reed parrotbill nests were  
634 more difficult to parasitize by cuckoos than were the nests of Oriental reed warblers.  
635 Therefore, the search for and approach to the nests of reed parrotbills were not  
636 important reasons for the low parasitism rate by cuckoos.

637 In addition, small scale nest or nest site characteristics may play a role in cuckoo  
638 host selection in our study area (Moskát and Honza 2000; Antonov et al. 2007). Host  
639 behavior can also be influential for explaining variation in cuckoo parasitism (Gill et  
640 al. 1997; Davies 2000). Warblers are noisy, aggressive and large birds, which are easy  
641 to detect. Parrotbills on the other hand are smaller and less conspicuous, and do not  
642 behave aggressively, which may make their nests more difficult for cuckoos to find  
643 (i.e., lower opportunity for eavesdropping on these hosts by cuckoos).

644



645 Thus, these various parameters seem additively decrease suitability of parrotbills  
646 as hosts leading to an apparent preference for other sympatric host (see Grim et al.  
647 2011). However, all these life history features can't complete explain the obvious  
648 deviation in the host use.

649 Previous studies have showed that many potential hosts escaped from cuckoo  
650 parasitism due to their aggressive defense against cuckoos when cuckoos approached  
651 their nests, as the first line of nest defense (Moksnes et al. 1991b; Røskaft et al. 2002;  
652 Welbergen and Davies 2009).

653 The dummy experiments disclosed that warblers, but not parrotbills responded  
654 aggressively to cuckoos. Further, parrotbills, in contrast to warblers, did not recognize  
655 cuckoos as a specific threat. The response of warblers to the intruders was consistent  
656 with previous work on closely related great reed warblers *Acrocephalus arundinaceus*  
657 in Europe (Honza et al. 2006; Trnka and Grim 2013). The significant differences  
658 between the responses of the two hosts in our study may imply that the Oriental reed  
659 warblers have a closer host-parasite relationship with common cuckoo than do reed  
660 parrotbills. There were two other main reasons for the lower level of aggression  
661 shown by reed parrotbills to the cuckoo dummy. First, the success of egg rejection  
662 during the egg brooding stage may represent a shift of anti-parasitism strategies from  
663 nest defense during egg laying to defense during the egg brooding stage, resulting in  
664 a failure of the parrotbills to recognize cuckoo adults. Secondly, the reed parrotbills  
665 may have lost the ability to recognize adult cuckoos during post-parasitism  
666 interactions with them, due to the lack of selection pressure to keep the trait.

667 Egg recognition experiments showed that there were no significant differences in  
668 the egg recognition ability by warblers and parrotbills, as both show a high rejection  
669 rate of non-mimetic eggs. However, the fact that the reed parrotbills show a much  
670 higher rejection rate of natural cuckoo eggs than warblers appears to be an important  
671 factor in explaining the apparent low parasitism rate on reed parrotbills in our study  
672 area and elsewhere (Yang et al. 2014). The rejection of cuckoo eggs by parrotbills has  
673 most likely evolved due to past parasitism by cuckoos and was not explained as a  
674 “collateral damage” (Samas et al. 2014) from adaptations against conspecific  
675 parasitism because (1) parrotbills rejected conspecific eggs rarely and at much lower  
676 rates than cuckoo eggs, and (2) we detected no cases of conspecific parasitism.  
677 However, cuckoos have not responded by evolving a mimetic egg. Hence, parrotbills  
678 are now difficult for cuckoos to successfully parasitize since their eggs are so different  
679 from the parrotbill eggs. Nevertheless, the well-developed egg recognition abilities in  
680 parrotbills suggest that they have been used by cuckoos in the past, and we cannot  
681 rule out that they still are hosts in parts of their breeding range. However, there is one  
682 cuckoo gens that mimic rufous-tailed shrike (*Lanius isabellinus*) eggs in the  
683 north-western part of China (Ma et al. 2012) with eggs that appear very similar to  
684 parrotbill eggs when judged by human eyes. Theoretically, shrike-race cuckoo might  
685 be successful in the invasion of the reed parrotbill if they had the opportunity to  
686 disperse their breeding scale to the reed habitat. This might be tested with egg  
687 experiments in the future.

688 Cross-fostering experiments showed that both hosts are equally good at raising

689 ~~cuckoo chicks as warblers. On the one hand, some samples in this study were large~~  
690 ~~and interspersed in space (study sites) and time (years). On the other hand, we~~  
691 ~~acknowledge that the sample sizes for chick growth were relatively small; however,~~  
692 ~~similar or smaller sample sizes were sufficient to reveal statistically highly significant~~  
693 ~~differences in cuckoo growth (Grim 2006) and even survival (Grim et al. 2009, 2011,~~  
694 ~~Yang et al. 2013) across different hosts. This suggests that our sample sizes were~~  
695 ~~representative and our conclusions are reliable. Hence, parrotbills should be good~~  
696 ~~quality hosts for cuckoos. The reason that the reed parrotbills have not evolved chick~~  
697 ~~discrimination to resist cuckoo parasitism during the nestling stage is most likely the~~  
698 ~~low evolutionary pressure due to the success of egg rejection at the earlier, egg laying~~  
699 ~~stage.~~

## 700 **Conclusion**

701 The host-specific parasitism in which the common cuckoo favoured Oriental reed  
702 warbler over reed parrotbill may be attributed to factors associated with both sides of  
703 the brood parasitism system (i.e., the initial selection by the cuckoo and constraints  
704 imposed by the hosts). In this study, we used a comprehensive approach to test the  
705 host responses to cuckoo parasitism at all developmental stages (e.g., adults, eggs,  
706 nestlings, ~~adults~~) and examined the influence of life-history traits that are not directly  
707 involved in parasite-host arms-races but still may affect their outcome. We showed  
708 that the main constraint preventing cuckoos from using reed parrotbills as hosts was  
709 the high frequency of egg rejection of non-mimetic cuckoo eggs. During the  
710 egg-laying stage specifically, the egg rejection rate reached ~90%, which may be

711 sufficient to make this host effectively secondarily unsuitable (~~se~~<sup>ensu</sup> Grim et al. 2011)  
712 for cuckoos. The egg rejection was the only successful anti-parasitism strategy; as  
713 there were no effective adaptations against cuckoo adults and chicks to counteract  
714 cuckoo parasitism in the reed parrotbill. However, we did find an obvious partial  
715 separation in the breeding time between the common cuckoo and the reed parrotbill,  
716 which would decrease the overall parasitism rate at the population level independently  
717 of other factors. Whether reed parrotbills have adopted an earlier breeding time in  
718 order to decrease the possibility of parasitism by cuckoos (Møller et al. 2011) is  
719 impossible to test directly but cannot be excluded. We suggest that future studies of  
720 host selection by parasitic birds will benefit from a comprehensive approach we used  
721 here, i.e. combination of observations and experiments across all developmental  
722 stages of parasite-host interactions.  
723

724 **Acknowledgements**

725 We are grateful to John A. Endler, Sara Helms Cahan and two anonymous referees for  
726 constructive comments that significantly improved the manuscript. We thank the  
727 Yellow River Delta Management Bureau for permission to undertake this study  
728 including all experimental procedures. The experiments comply with the current laws  
729 of China. We are particularly grateful to two French volunteers (Andrieu Julie and  
730 Marion Soresina) for their help with data collection in the field; Yueliang Liu, Shuyu  
731 Zhu, Kai San, Xianghai Du, Shuyi Zhang, and Pengfei Guo for their kind support, and  
732 Baoshan Cui for sharing the laboratory in the field station. We would also like to  
733 thank Chao Li (Gudong Oil Production Plant, Sinopec Shengli Oilfield), Junlin Chen  
734 (Anhui University), Xianxian Liu, Xiaomei Shen, and Qiao Wu for their kind help  
735 during this study. This work was supported by the National Natural Science  
736 Foundation of China (Nos. 31301888 to DL; 31272328 and 31472013 to WL), Open  
737 Fund of Ministry of Education Key Laboratory for Biodiversity Sciences and  
738 Ecological Engineering, Beijing Normal University (K1401 to DL), General scientific  
739 research project of Education Department of Liaoning Province (L2015196 to DL),  
740 National Basic Research Program of China (2006CB403305 to ZZ) and United  
741 Foundation for Natural Science of National Natural Science Foundation of China and  
742 People's Government of Guangdong Province (U0833005 to ZZ). BGS was funded by  
743 the Research Council of Norway (218144). TG acknowledges the support from  
744 Human Frontier Science Program (awards RGY69/2007 and RGY83/2012) and the  
745 Czech Science Foundation (grant no. P506/12/2404). We declare that all authors have  
746 no conflict of interest.



748

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950



951

952 **Figure legends**

953 **Figure 1.** Nests of reed parrotbill (a, c) and Oriental reed warbler (b, d).

954

955 **Figure 2.** Host responses to dummies quantified on ordinal (a) and continuous scales

956 (b).

957

958 **Figure 3.** Background color and spots of eggs of the common cuckoo (n = 19) and its

959 two hosts (warblers: n = 55; parrotbills: n = 14): (a) reflectance spectra (300–700 nm;

960 0.597-nm intervals) of background color and spots, (b) the difference between light

961 spots (LS), corresponding to the square frame in red), and dark spots (DS),

962 corresponding to the square frame in yellow.

963

964 **Figure 4.** Host responses to egg experiments: acceptance (white), desertion (grey),

965 ejection (black). Sample sizes given within bars.

966

967 **Figure 5.** The growth (body mass, g) of common cuckoo chicks raised by two hosts:

968 (a) the filled circles and black solid line represent cuckoo chicks in the original (i.e.,

969 naturally parasitized) warbler nests (n = 15); the hollow circles and grey solid line

970 represent cuckoo chicks ~~the~~-cross-fostered between warbler nests (n = 5); (b) the

971 triangle and the dotted line represent cuckoo chicks ~~the~~-cross-fostered from warbler

972 to parrotbill nests (n = 6).

973

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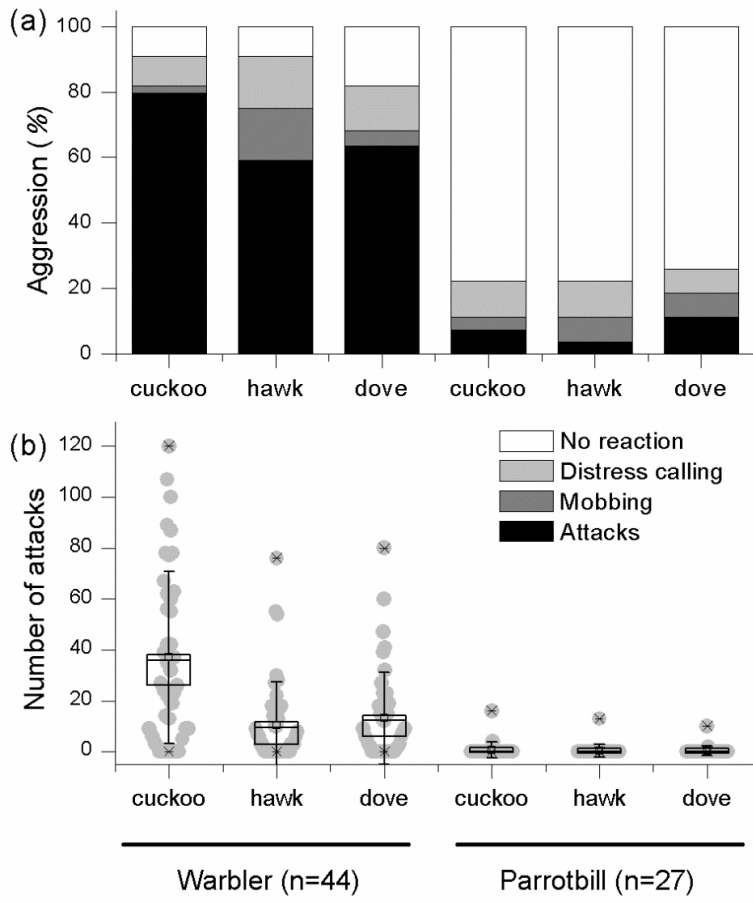


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977 **Fig. 1**

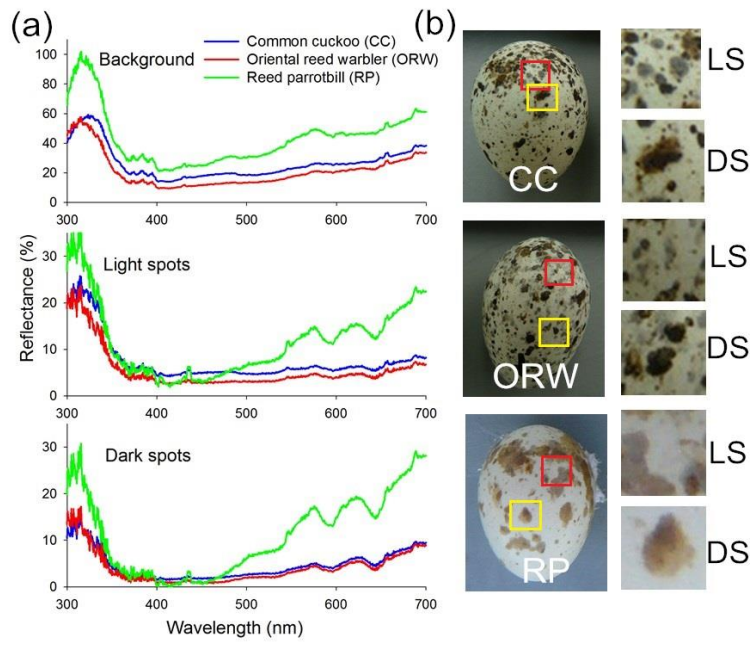
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983 **Fig. 2**  
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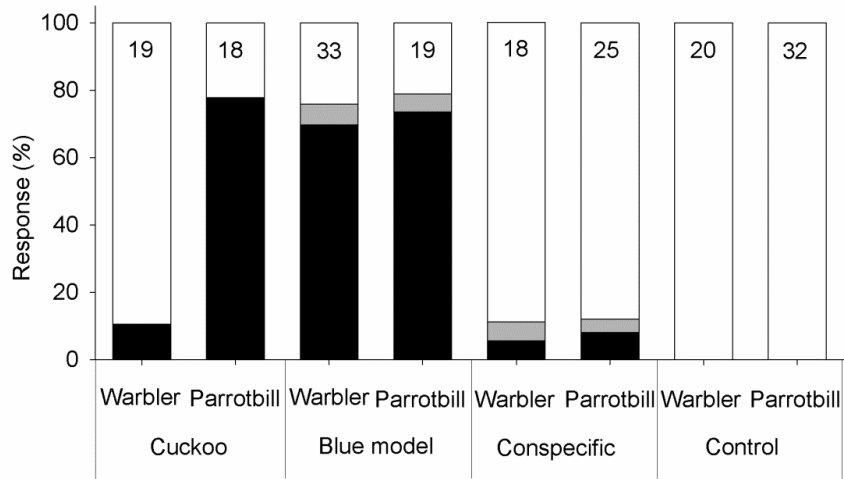


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987 **Fig. 3**

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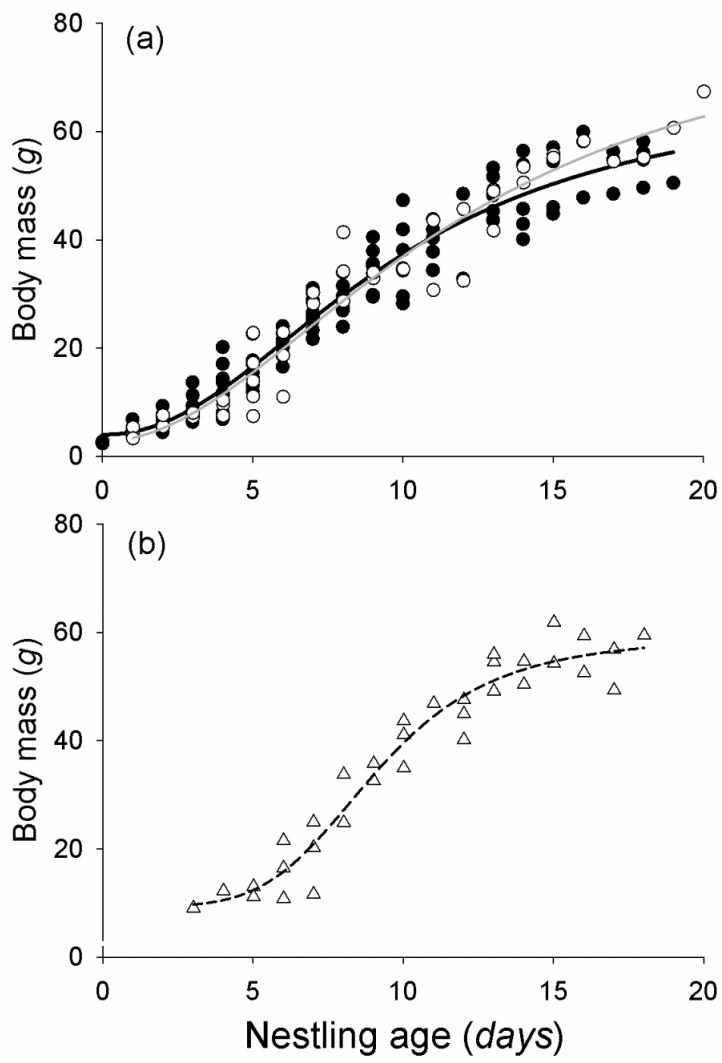
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992 **Fig. 4**

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998 **Fig. 5**

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1002 **Table legends**

1003

1004 ~~**Table 1.** Cuckoo parasitism rates on Oriental reed warblers and reed parrotbills in the~~

1005 ~~Yellow River delta, Eastern China.~~

1006

1007 **Table 21.** Effects of nest sites and nest characteristics on cuckoo parasitism on

1008 Oriental reed warblers and reed parrotbills in the Yellow River delta, Eastern China.

1009

1010 **Table 2.** Cuckoo chicks survival in naturally and experimentally parasitized nests of

1011 Oriental reed warblers and reed parrotbills.

1012

1013 **Table 3.** Basic growth parameters for cuckoo chicks raised by Oriental reed warblers

1014 and reed parrotbills.

1015 ~~**Table 3.** Fate of cuckoo chicks cross fostered in the nests of Oriental reed warblers~~

1016 ~~and reed parrotbills in the Yellow River delta, Eastern China.~~

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1021 **Table 1.** Effects of nest sites and nest characteristics on cuckoo parasitism on Oriental reed warblers and reed parrotbills in the Yellow River  
 1022 delta, Eastern China. Sample sizes (nest number) given in parentheses.

Nest sites and nest characteristics	Parasitized warblers	Non-parasitized warblers	Reed parrotbills	Parasitized warblers vs non-parasitized warblers	Parasitized warblers vs parrotbills	Non-parasitized warblers vs parrotbills
Distance to perch (m)	59.31 ± 11.42 (83)	106.39 ± 9.06 (240)	88.58 ± 11.31 (173)	t = 2.80, p = 0.005	t = -1.61, p = 0.108	t = 1.10, p = 0.247
Distance to reed edge (m)	5.52 ± 1.23 (39)	6.69 ± 0.75 (118)	3.36 ± 0.23 (143)	z = -0.97, p = 0.33	z = -0.56, p = 0.563	z = -2.40, p = 0.017
Nest visibility by observer	3.51 ± 0.19 (40)	3.32 ± 0.11 (162)	2.92 ± 0.12 (143)	z = -0.91, p = 0.36	z = -2.44, p = 0.015	z = -2.45, p = 0.014
Height of reed above the nests (m)	1.44 ± 0.04 (39)	1.55 ± 0.09 (120)	0.65 ± 0.03 (142)	z = -0.39, p = 0.70	z = -7.26, p < 0.0001	z = -8.25, p < 0.0001
Number of reed stems	27.40 ± 1.93 (40)	26.17 ± 0.99 (122)	15.56 ± 0.85 (143)	t = -0.60, p = 0.55	t = 6.23, p < 0.0001	t = 8.18, p < 0.0001
Mean height of reed (m)	2.45 ± 0.10 (40)	2.45 ± 0.06 (122)	1.89 ± 0.03 (143)	z = -0.90, p = 0.37	z = -7.70, p < 0.0001	z = -10.35, p < 0.0001
Percentage of dry reed stem	10.37 ± 3.49 (40)	10.24 ± 1.71 (122)	33.07 ± 1.34 (143)	z = -0.01, p = 1.00	z = -6.55, p < 0.0001	z = -9.07, p < 0.0001
Height of nest above water or ground (m)	0.98 ± 0.04 (39)	0.97 ± 0.03 (120)	0.63 ± 0.01 (142)	t = -0.30, p = 0.76	t = 10.08, p < 0.0001	t = 11.61, p < 0.0001
Volume of nest (cm <sup>3</sup> )	876.53 ± 50.48 (37)	893.52 ± 27.95 (116)	488.47 ± 20.93 (48)	t = 0.30, p = 0.77	t = 7.72, p < 0.0001	t = 8.89, p < 0.0001

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1027 **Table 2.** Cuckoo chicks survival in naturally and experimentally parasitized nests of Oriental reed warblers and reed parrotbills.

Treatment	Fate of cuckoo chicks (%)		
	Successfully fledged	Predated	Nest failure due to bad weather
Warblers – natural parasitism (n = 18)	44	33	22
Warblers – cross-fostered (n = 8)	38	63	0
Parrotbills – cross-fostered (n = 6)	33	50	17

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1031 **Table 3.** Basic growth parameters for cuckoo chicks raised by Oriental reed warblers and reed parrotbills.

Measures	Growth parameters	NW (n = 6)	CW (n = 2)	CP (n = 4)	Statistic values
Body mass	<i>A</i>	56.28 ± 3.42	61.51 ± 2.00	59.82 ± 5.39	$F_{2,11} = 0.35, p = 0.72$
	<i>K</i>	0.37 ± 0.03	0.33 ± 0.02	0.39 ± 0.05	$F_{2,11} = 0.36, p = 0.71$
	<i>t<sub>i</sub></i>	7.89 ± 0.69	8.35 ± 0.16	7.79 ± 0.80	$F_{2,11} = 0.07, p = 0.93$
Tarsus length	<i>A</i>	25.52 ± 0.62	26.64 ± 0.22	24.53 ± 1.36*	$F_{2,10} = 0.95, p = 0.43$
	<i>K</i>	0.30 ± 0.02	0.26 ± 0.01	0.30 ± 0.02*	$F_{2,10} = 0.48, p = 0.64$
	<i>t<sub>i</sub></i>	4.11 ± 0.78	3.75 ± 0.23	3.53 ± 0.55*	$F_{2,10} = 0.15, p = 0.87$

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1033 Notes: The growth parameters were estimated using nonlinear regression to fit the body measures (mass and tarsus length) to logistic function:

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$$W(t) = A / (1 + e^{(-K(t-t_i))})$$

1035 where  $W(t)$  is body measure at age  $t$ ,  $A$  is the asymptotic body measures,  $K$  is a measure of growth rate, and  $t_i$  is the inflection point on the growth

1036 curve (Starck and Ricklefs 1998). The logistic growth curves were fitted for each individual nestling that survived for at least 14 days post-hatch

1037 (hatching day = 0). Differences tested with ANOVAs (Kruskal-Wallis tests led to same conclusions). Values are means ± SE. NW natural

1038 parasitized warblers, CW cross-foster warblers, CP cross-foster parrotbills. \* the sample size is 3.

**Reply to comments (EVEC-D-15-00179)**

**Dear Prof. Endler,**

**Thank you very much for kindly giving us the chance to revise our manuscript (EVEC-D-15-00179). We have read the comments carefully and have revised the paper as suggested by you, the Associate Editor, Sara Helms Cahan, and the two reviewers. This has resulted in a more balanced and focused paper, and we hope that you agree with this assessment. Please find explained with blue bold font below how we have addressed these points.**

**Thank you very much in advance for your editorial assistance.**

**Yours sincerely, on behalf of the authors,**

**Wei Liang**

Dear Dr. Liang,

I have received the reviews of your manuscript, "Explaining variation in brood parasitism rates between potential host species with similar habitat requirements", submitted to *Evolutionary Ecology*. The comments are found after this letter, below.

As you will see, although the body of the paper was good, the discussion was seriously flawed, even self-contradictory in places. You need to totally rethink the organisation and presentation/interpretation of the results to make them consistent with the data and with the entire data set.

Please fix these problems, and I expect to be able to accept the manuscript when you have corrected them. Please submit a cover letter with the revision saying what you did; and if you did not follow suggestions, say why.

If you need more time than automatically assigned by the Editorial Manager, please let me know. I would rather wait longer for a better paper.

Please submit your revised manuscript online by using the Editorial Manager system which can be accessed at: <http://evec.edmgr.com/>

Revised manuscripts that are accepted for publication will be checked by our copyeditors for spelling and formal style; however, this may not be sufficient if English is not your native language, and substantial editing might be required. In that case, you may want to have your manuscript edited by a native speaker prior to submitting the revised version.

The revised and accepted manuscript will become the final version of record, and it is

the author's responsibility to ensure that this version is free of any kinds of errors. Do not assume that we do detailed copy-editing. Assume that what you send in will be published essentially as is.

Please make sure to submit your editable source files (i. e. Word, TeX); we can NOT use PDF files.

I am looking forward to receiving your revised manuscript before 29 May 2016.

With kind regards,

John A Endler  
Editor in Chief  
Evolutionary Ecology

#### COMMENTS FOR THE AUTHOR:

Associate Editor's comments: this study is a comprehensive comparison of two sympatric potential avian host species whose realized parasitism rates differ significantly. The number of factors analyzed was impressive, and overall I found the manuscript clear and easy to read. The big exception to this, however, was the discussion, which flipped back and forth among different preferred hypotheses and at times appeared to contradict claims made elsewhere in the manuscript (e.g., the role of egg rejection). A revision would require a re-evaluation of the structure and content of the discussion to make clear what the results do and do not show, and how different mechanisms interact with one another over the course of host specialization (ie did breeding asynchrony/low density lead to evolutionary shifts toward matching the eggs of the more available warbler, further reducing parrotbill acceptance, or is warbler egg matching the ancestral condition, such that egg rejection has been consistently the predominant factor maintaining differential host use?). It may be the case that the comparative data presented here cannot really tease this apart, but if so, this should be made clear.

Both reviewers make some useful suggestions regarding analysis of existing data and literature on other systems that should be utilized, which I would encourage the authors to consider.

Sincerely,  
Sara Helms Cahan

#### **Reply:**

**Thank you very much for your helpful comments. We have made major changes to the structure and content of the discussion following your suggestions. Please see the revised Discussion (Lines 465-699).**

Reviewer #1: Here the authors present an exhaustive set of experiments and correlative observations to determine the cause(s) for cuckoo host choice between two sympatric host species. The manuscript is well-written and presents one of the most comprehensive studies of host selection to date. This study will surely be influential to future research; not only setting the example of what needs to be evaluated to attempt to answer this complicated question, but also providing inference on the evolution of host selectivity.

**Reply:**

**Thank you very much for your kind words.**

My main concern is that the discussion seemed to partially disregard the importance of egg rejection by parrotbills in host choice decisions by cuckoos. Granted, the abstract and conclusion state that cuckoo eggs were mostly accepted by warblers, but rejected by parrotbills. Yet the discussion in its current form dispels many alternative hypotheses (habitat imprinting, host seasonality, host aggression, etc.) and then appears to point mostly to the density of hosts as an influential factor for host selectivity. While the density hypothesis is intriguing, I find it unconvincing given the experimental design. To explore this idea as well as the other hypotheses tested, I would expect a kernel estimate of density (rather than nests/total area) and a temporal aspect where the density was measured during the cuckoo's breeding season.

**Reply:**

**As for alternative hypotheses: we agree with you and we completely rephrased the whole Discussion. We now stress that no single parameter fully explains host selection in our study system; see, e.g., that "not only one but rather several mechanisms may additively and interactively render parrotbills less suitable to cuckoos than warblers".**

**As for density estimates: we acknowledge there are various ways how to estimate breeding density. We followed the straightforward method used by, e.g., Samaš et al. 2013, which is reliable because it directly takes into account all simultaneously active nests that are available to cuckoos in the peak part of the season. Thus, "temporal aspect" noted by you has been taken into account. We added this explanation to the revised ms.**

This idea could also be compared amongst warblers; does the variation in warbler density predict cuckoo parasitism? Furthermore, we must assume that an equal proportion of nests were found between each host species, therefore a point-count estimate of density would also be helpful to test this hypothesis. Looking at Area A (Fig. S1), it appears that the densities of each species are nearly equal, yet parasitism rates are still very different. While the density hypothesis is indeed possible, I suggest that a more nuanced view should be presented in the discussion, with more focus on the relationship of reproductive success/fitness influencing host choice decisions. This leads to interesting implications--Do individual cuckoos learn which hosts are more

likely to accept through trial-and-error, or do young cuckoos imprint on their hosts that ultimately leads to differential parasitism through population differences?

**Reply:**

**The question about "trial-and-error" and "imprinting" is fascinating but far beyond the scope of our study. In fact, despite hundreds of studies published on the common cuckoos in recent years, the mechanism of host choice (at the level you refer to) remains enigmatic.**

Again, I am amazed by this study and found it a pleasure to read! I hope my comments have helped in some way.

**Reply:**

**Thank very much for your positive words and very helpful comments. We have revised the discussion with more focus on the relationship of reproductive success/fitness influencing host choice decisions, and also put more emphasis on alternative hypotheses explaining host selection by cuckoos as you suggested. Please see Lines 465-699.**

Minor comments:

Line 328: warblers that were parasitized were more like to place their nests...

**Reply:**

**Thanks for this suggestion. After having re-read the whole sentence, we found it to be a bit awkwardly presented on our behalf leading to confusion. We have therefore changed wording. Regarding distance to reed edge: From table 1 it is apparent that warblers in general tended to breed further away from reed edge, but only significantly so when comparing non-parasitized warblers versus parrotbills. Please see Lines 350-354.**

Reviewer #2: This manuscript examines host choice by cuckoos. The authors examine life history traits of two sympatric species, the Reed Parrotbill and Oriental Reed Warbler, in an attempt to explain the differential parasitism frequencies. While the authors suggest such comprehensive studies have not been done on cuckoo hosts, there are at least two similar studies that have been done on cowbird hosts (Peer and Bollinger 1997, Condor 99:151-161; Ortega and Cruz Auk 108:16-24). The authors found that density, high rejection frequency, and non-overlapping breeding seasons all may contribute to the lower parasitism on Parrotbills. I have relatively few comments listed below.

**Reply: Thank you very much for your helpful comments. We have added citation to the two studies following your suggestions (please see Lines 65-72).**

Specific Comments:

103: It's unclear what you mean by "full reality". Please re-phrase.

**Reply:**

**Thank you. We have re-phrased this sentence. Please see Lines 105-109.**

156: You should justify using this system based on the methodological suggestions of Sealy et al. (1998; Pp.194-211 in Parasitic birds and their hosts: studies in coevolution [S.I. Rothstein and S. K. Robinson]).

**Reply:**

**Thanks. Revised. And we moved insertion above because Sealy et al. (1998) used different scales, not ordinal ones. Please see Line 150 and Lines 163-170, 174-179.**

165-172: Because you are interested in nest features, it would have also been interesting to collect data on reflectance of the nest linings of the two species.

**Reply: Thanks. We agree in that this would be very interesting indeed. Unfortunately, we do not at present possess such data, but this should surely be the scope for future study.**

401-402: Please clarify if it is the birds' physical inability to reject the eggs or their inability to recognize them that resulted in acceptance.

**Reply:**

**Thank you. We did not video-record responses to introduced eggs, but the data strongly suggest that parrotbills were able to recognize both cuckoo and model eggs. Hence, these two types were rejected at approx. the same rates, but with highly different outcome as explained in the text. Oriental reed warblers and reed parrotbills have distinctly different bill morphology (Xiong & Lu 2013, added to References). Due to their short and blunt bills, parrotbills are most probably not able to grasp eject eggs and therefore have to rely on puncture ejection (or desertion). This seemed to work fine on real cuckoo eggs, but they faced problems when trying to get rid of the thicker-shelled model eggs. Warblers, on the other hand, should be able to grasp eject eggs (see e.g. Antonov et al. 2006 for video recordings of ejection in great reed warblers and three smaller *Acrocephalus* warblers, added to references), or puncture and remove even hard-shelled model eggs (see Honza & Moskat 2008, added to references). These results taken together strongly suggest that the "forced acceptance" of model eggs by parrotbills were simply due to their inability to remove such eggs (even though they were pecked, i.e. we observed pecking marks on the surface of the eggs). We have revised the text in order to explain this. Please see Lines 424-426 and 436-446.**



443: This is very similar to the situation with Brown-headed Cowbirds and Common Grackles (mentioned above). Grackles breed very early, and it may contribute to the lack of parasitism on them, but isn't the sole or primary reason for the lack of parasitism.

**Reply:**

**Thank you very much for your interesting information. We have added a citation here. Please see Lines 517-518.**