

1 No reproductive fitness benefits of dear enemy behaviour in a territorial songbird

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19

20 ABSTRACT

21

22 Territorial animals often respond less aggressively to neighbours than strangers. This 'dear enemy' effect  
23 is hypothesized to be adaptive by reducing unnecessary aggressive interactions with non-threatening  
24 individuals. A key prediction of this hypothesis, that individual fitness will be affected by variation in the  
25 speed and the extent to which individuals reduce their aggression towards neighbours relative to  
26 strangers, has never been tested. We used a series of song playbacks to measure the change in response  
27 of male great tits to a simulated establishment of a neighbour on an adjacent territory during early  
28 stages of breeding, as an assay of individuals' tendencies to form dear enemy relationships. Males  
29 reduced their approach to the speaker and sang fewer songs on later playback repetitions. However,  
30 only some males exhibited dear enemy behaviour by responding more strongly to a subsequent stranger  
31 playback, and when the playback procedure was repeated on a subset of males, there was some  
32 indication for consistent differences among individuals in the expression of dear enemy behaviour. We  
33 monitored nests and analysed offspring paternity to determine male reproductive success. Individuals  
34 that exhibited dear enemy behaviour towards the simulated neighbour did not suffer any costs  
35 associated with loss of paternity, but there was also no evidence of reproductive benefits, and no net  
36 effect on reproductive fitness. The general ability to discriminate between neighbours and strangers is  
37 likely adaptive, but benefits are probably difficult to detect because of the indirect link between  
38 individual variation in dear enemy behaviour and reproductive fitness, and because of the complex  
39 range of mechanisms affecting relations with territorial neighbours.

40

41 Key words: habituation, individual recognition, playback, great tit, territorial behaviour, cognition

42

43 INTRODUCTION

44

45 Territoriality is a widespread behaviour that provides important benefits to territory holders such as  
46 reducing competition for food or breeding resources, and guarding of mates from extra-pair matings  
47 (Stamps 1994; Adams 2001). However, there are many costs to holding territories that arise primarily  
48 from the vigilance and aggressive behaviours required to defend and maintain territorial boundaries  
49 against intruders (Ydenberg 1984; Mares et al. 2012; Wischhoff et al. 2018). One way to lower these  
50 costs is to reduce territorial defence behaviours towards non-threatening individuals and instead focus  
51 defence efforts particularly on those individuals that pose a threat of usurping the territory or the  
52 resources within (Getty 1987; Temeles 1994). Thus, many species exhibit the ‘dear enemy effect’, which  
53 is defined as individuals showing less aggressive behaviour towards territorial neighbours than towards  
54 strangers (Ydenberg et al. 1988; Temeles 1994; Stoddard 1996; Tumulty 2018). If neighbours are not a  
55 threat because they hold their own territory, then dear enemy behaviour should benefit individual  
56 fitness through reduced costs of unnecessary aggression, facilitating greater investment in foraging and  
57 reproduction (Getty 1987; Temeles 1994), as well as defence against truly threatening individuals (Leiser  
58 and Itzkowitz 1999). This hypothesis predicts that intraspecific variation in the speed and extent to  
59 which individuals reduce their aggression towards non-threatening neighbours will affect individual  
60 fitness, particularly enhancing reproductive success when the territory is used for breeding. However,  
61 this key prediction has never been tested.

62

63 Selection acts on individual variation, and thus to understand the evolution of the dear enemy effect it is  
64 important to determine whether individuals differ consistently in dear enemy behaviour (as a proxy for  
65 heritability), and whether these differences have fitness consequences. Repeatable individual variation  
66 in dear enemy effect expression is expected because of variation in individuals’ cognitive capabilities to

67 recognize familiar neighbours (Reichert and Quinn 2017), because of personality traits such as  
68 aggressiveness (Akçay et al. 2014), and due to covariance with other repeatable behavioural traits  
69 (Verbeek et al. 1996). Some studies have provided indirect support for fitness benefits of dear enemy  
70 behaviour, for instance by demonstrating that individuals holding territories with long-term neighbours  
71 have higher reproductive success than those with new neighbours, or that neighbours tend to engage in  
72 cooperative behaviours together (Beletsky and Orians 1989; Grabowska-Zhang et al. 2012a, b; Siracusa  
73 et al. 2021). However, in these studies it is unknown whether and to what extent individuals  
74 discriminated between neighbours and strangers in their aggressive interactions, and therefore whether  
75 there was variation in dear enemy behaviour. Thus, while it is clear that the ability and tendency to  
76 discriminate neighbours from strangers varies and likely has functional significance, there is still a  
77 limited understanding of the selection pressures that may be acting on dear enemy behaviour,  
78 especially at the within-species level.

79  
80 The dear enemy effect is facilitated by cognitive mechanisms that enable individuals to learn some  
81 characteristic of their neighbours, allowing them to discriminate between neighbours and strangers  
82 (Wiley 2013). These mechanisms – of which more than one may be involved in any given species – range  
83 from habituation to a neighbour's signal characteristics and/or their spatial location (Petrinovich and  
84 Peeke 1973; Brooks and Falls 1975; Yasukawa 1981; Bee and Gerhardt 2001; Dong and Clayton 2009),  
85 associative learning of neighbour characteristics (Richards 1979), to 'true individual recognition'  
86 (Johnston and Jernigan 1994; Gheusi et al. 1997; Saeki et al. 2018), and act over time scales ranging from  
87 short-term decreases in aggression within a day to persistent recognition of individuals across years  
88 (Godard 1991; Tumulty and Sheehan 2020). Thus, variation among individuals in the expression of the  
89 dear enemy effect (i.e. the extent and speed with which aggression is reduced towards neighbours  
90 relative to strangers) may arise because of variation in the cognitive abilities associated with neighbour-

91 stranger discrimination. If this cognitive variation affects reproductive success—for instance if those  
92 individuals on breeding territories that quickly learn to recognize their neighbours avoid unnecessary  
93 agonistic encounters and can invest more in their offspring—then individuals with superior cognitive  
94 ability may have higher fitness and be favoured by selection. Non-cognitive factors also affect the  
95 expression of the dear enemy effect. For instance, individuals may differ in aggressiveness or other  
96 personality traits (Hyman et al. 2004; Amy et al. 2010; Jacobs et al. 2014), and context-dependent  
97 factors such as territory size, breeding status, and the density of neighbouring territory-holders also  
98 likely affect responsiveness to neighbours (Werba et al. 2021). Regardless of the source, this individual  
99 variation in dear enemy expression has potentially significant, but unexplored, consequences for fitness.  
100 Furthermore, few studies have examined the trajectory over which the dear enemy effect develops  
101 upon establishment of a new neighbour (e.g., Bee and Gerhardt 2001), or whether this differs among  
102 individuals.

103  
104 Like many songbirds, great tits (*Parus major*) defend territories around their nest during the breeding  
105 season (Gosler 1993). Male great tits do so by singing and approaching intruding individuals to engage in  
106 visual displays and occasionally, physical fighting (Blurton Jones 1968; Krebs 1977). Great tits nest in  
107 natural cavities or artificial nest boxes, and the primary threat from intruders is the potential for them to  
108 usurp the limited resource of a high-quality nesting location (Krebs 1971, 1976, 1982), although  
109 intruders also present other threats including potentially mating with the territory-holder's social mate  
110 (Hill et al. 2011) or foraging on the territory (Hinde 1956). In great tits, approximately 25-50% of broods  
111 contain extrapair young (Lubjuhn et al. 1999; Brommer et al. 2010; Patrick et al. 2012). The dear enemy  
112 effect has been demonstrated previously in great tits: in playback experiments, individuals showed a  
113 reduced response to songs of their territorial neighbours compared to songs of strangers (Krebs 1971;  
114 Falls et al. 1982; McGregor and Avery 1986), and the effect was stronger when the neighbour's song was

115 played from its own territory (McGregor and Avery 1986). Territory defence begins very quickly after  
116 settlement, often within hours (Krebs 1971). The speed with which dear enemy relationships are formed  
117 is unknown, but given that strong territory defence occurs during a limited breeding season, and that  
118 great tits habituate rapidly to song (Krebs 1976), a reduced response to neighbours compared to  
119 strangers is likely to occur within a few days.

120  
121 Recognition of neighbours in great tits is not based on a simple discrimination between the categories of  
122 familiar and unfamiliar individuals (Wiley 2013); instead they can learn to discriminate among the songs  
123 of different specific individuals (McGregor and Avery 1986; Weary and Krebs 1992). There is also among-  
124 individual variation in aggressive responses to playback resulting from personality differences (Amy et  
125 al. 2010), and personality and reproductive investment were related to the speed with which individuals  
126 habituated to a series of song playbacks (Rivera-Gutierrez et al. 2017); this habituation to a familiar  
127 stimulus is likely an important mechanism in the establishment of dear enemy relations (Peeke 1984).  
128 Great tits trade off the time invested in foraging and territory defence (Ydenberg 1984; Ydenberg and  
129 Krebs 1987); thus, individuals that rapidly reduce their aggression towards their neighbours may benefit  
130 directly by increasing their foraging intake, and this in turn could enhance their ability to provision for  
131 their offspring (Martin 1987). However, vigilance must be maintained against potential territorial  
132 usurpers, because the longer a usurper is on the territory, the more effort is required to expel it (Krebs  
133 1982).

134  
135 We performed a series of acoustic playback experiments in which we monitored territorial males'  
136 responses to the simulated arrival of a new male on a neighbouring territory. Our overall objective was  
137 to examine whether individuals habituated by reducing their response after repeated exposures to the  
138 songs of a simulated new neighbour while still maintaining a heightened response to a stranger (i.e.,

139 displayed dear enemy behaviour), whether they differed consistently in this regard, and whether there  
140 were any beneficial effects of the tendency to form dear enemy relationships on fitness and  
141 reproduction in general. We note that we did not expect these fitness effects to arise because of the  
142 individual's actual behaviours towards the simulated neighbour in our playback trials, but rather we  
143 assumed that the individual's behaviour in the playback trials was indicative of how it engaged with  
144 others in natural territorial interactions, with variation in the tendency to reduce aggression towards a  
145 familiar stimulus (as an experimental proxy for the tendency to form dear enemy relationships) leading  
146 to effects on reproductive success.

147

148 First, we determined if males' responses to playbacks of a simulated neighbour that were broadcast  
149 multiple times across three days declined over time, consistent with habituation to the neighbour  
150 playback stimulus. Second, we tested whether the response to a subsequent 'stranger' playback was  
151 stronger than that to the final neighbour playback, consistent with the reduced aggressive response to a  
152 familiar neighbour compared to a stranger that is the hallmark of the dear enemy effect. Third, we  
153 estimated the repeatability of several dear enemy behaviour measures to determine if individuals  
154 differed intrinsically in these behaviours. We also explored the extent to which the expression of these  
155 dear enemy behaviour measures was context dependent, for example due to phenology, which is  
156 related to overall levels of nest defence (Hyman 2005; Jin et al. 2021), and the repetition rate of songs  
157 during the playback, which affects the rate of habituation towards repeated stimuli (Thompson et al.  
158 1973). Finally, we tested whether there was any evidence for selection or any reproductive benefits of  
159 dear enemy behaviour in a number of ways: A) controlling for paternity, we tested the prediction of  
160 positive selection on the tendency to perform dear enemy behaviour, that is, that individuals that  
161 rapidly reduced their response to neighbours should fare better for a variety of life history traits that are  
162 good indicators of reproductive fitness and recruitment to the breeding population in the great tit

163 (Tinbergen and Boerlijst 1990), in particular clutch size, the number of offspring fledged, and average  
164 offspring mass; B) We repeated these analyses including all nestlings (including extra-pair) to test for  
165 evidence of any benefits of the tendency to perform dear enemy behaviour at the nest, irrespective of  
166 paternity; C) We examined if there was any relationship between observed levels of extra-pair paternity  
167 at the social nest and the tendency to perform dear enemy behaviour. We discuss the implications of  
168 our experimental results and analyses of reproductive success for our understanding of the dear enemy  
169 effect.

170

## 171 METHODS

172

173 Playbacks were performed during the spring breeding season (April-May in 2017 and 2018) in eight  
174 small forestry plots in County Cork, Ireland (Table S1, Fig. S1). Each site contained an array of nestboxes,  
175 which are preferentially used by great tits for breeding (East and Perrins 1988), and in which most  
176 individuals had been ringed as part of a long-term study (for details see O'Shea et al. 2018). We  
177 identified potential playback subjects by listening for males singing near nestboxes and examining the  
178 progress of nest building in the box. Males chosen for the experiment were then subject to a series of  
179 song playbacks as described below.

180

### 181 *Playback stimuli*

182

183 Male great tits sing on territories containing their nesting site. They typically have a repertoire of three  
184 to four distinctive song types (Gompertz 1961; McGregor and Krebs 1982a) but usually repeat the same  
185 one for several minutes before switching to a different type (Krebs 1976). The playbacks were designed  
186 to mimic this repetition of a single song type. Although simulating a larger song repertoire through



187 playbacks may have captured additional aspects of the dear enemy phenomenon, this was not  
188 necessary to address our primary aims and would have reduced our power to detect dear enemy  
189 behaviour because: 1. Males habituate to the presentation of both a single song type and multiple song  
190 types, but habituation is slower to playback of multiple song types (Krebs 1976), and 2. Males will  
191 respond to the presentation of a single song type in a manner consistent with the dear enemy effect:  
192 responding more strongly to a single song type of a stranger than to a single song type of an established  
193 neighbour (Krebs 1971), 3. Great tits are capable of discriminating between individuals even based on  
194 songs of those individuals they have never heard before (Weary and Krebs 1992). Thus, our comparison  
195 of birds' responses to a simulated neighbour (recorded song from one individual, played back several  
196 times) and a simulated stranger (recorded song from a different individual, played back once) is an  
197 appropriate assay of dear enemy behaviour (i.e., the difference in response to a familiar stimulus from a  
198 familiar location, the neighbour, and an unfamiliar stimulus from an unfamiliar location, the stranger)  
199 and is unlikely to have been perceived by the bird as two different song types from the same individual.

200  
201 The playback stimuli consisted of recordings of natural male songs made using Wildlife Acoustics SM4  
202 audio recorders (24 kHz sampling rate) placed at nestboxes in May 2016. We scanned audio files for  
203 exemplars of male songs with a high signal to noise ratio and containing no other bird songs in the  
204 background. We inserted each chosen song into a new audio file in Audacity software, bandpass filtered  
205 the song between 1.5 and 11.5 kHz, and manipulated the song to contain 6 phrases (the basic repeating  
206 unit of the song (McGregor and Krebs 1982b)) by copying or deleting phrases as needed. The song  
207 exemplar was then copied so that it was played back at a rate of either five or ten songs per minute for  
208 five minutes, which we refer to as the "low" and "high" stimulus rate treatments, respectively. These  
209 two stimulus rates were used to test the prediction that the likelihood of habituation to the neighbour  
210 songs depended on the stimulus repetition rate (Thompson and Spencer 1966). A total of 29 song

211 exemplars were chosen, and each exemplar was recorded at a different nestbox; songs came from seven  
212 of the eight study sites. The playback stimulus selected for the subject male and the song rate treatment  
213 were chosen randomly, with the restriction that the stimulus song was not recorded from the same site  
214 as the subject (all sites were at least 2.25 km apart from each other; Table S1). This ensured that  
215 subjects would not have been familiar with the playback song already. Stimuli were broadcast as .wav  
216 files from an EasyAcc X02s speaker mounted on a tripod at approximately 1 m height, at a sound-  
217 pressure level of 90 dB (A) measured at 1 m using an Extech 407730 sound level meter. Great tit males  
218 respond readily to playback of song exemplars by exhibiting territorial behaviour (Rivera-Gutierrez et al.  
219 2015; Snijders et al. 2017; Jin et al. 2021).

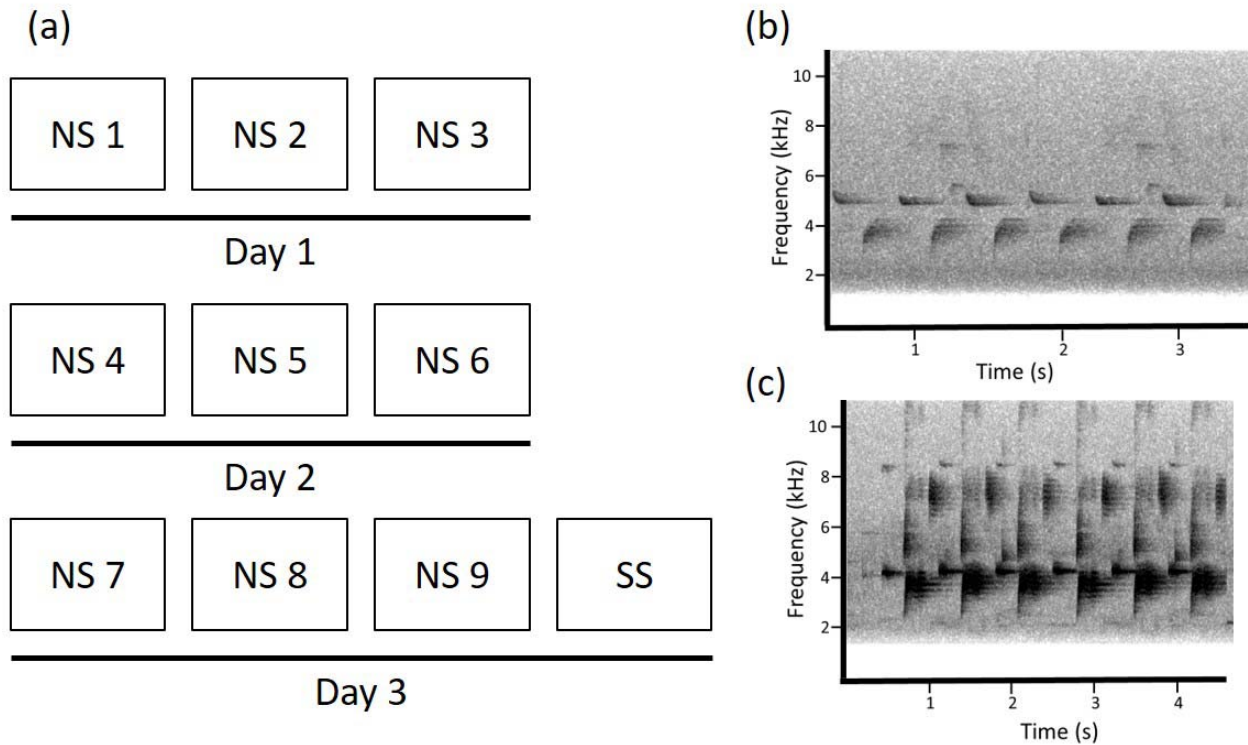
220

### 221 *Experimental design*

222

223 On each of three consecutive days we exposed males to three playbacks, performed at 1-hour intervals,  
224 of one of the playback stimuli (Fig. 1). Each subject was therefore exposed to a total of nine playbacks of  
225 the same stimulus (henceforth the “neighbour” stimulus), which simulated a newly arrived male on a  
226 neighbouring territory. Territory settlement generally takes place very rapidly in this species (Krebs  
227 1971), and responses to repeated playback typically decrease over a few days (Krebs et al. 1981; Rivera-  
228 Gutierrez et al. 2017), so this interval allowed us to study the initial development of dear enemy  
229 behaviour. The playbacks were always performed from the same location, and at a distance of 25 m  
230 from the nestbox. This location was chosen because territoriality is likely strongest near the nestbox  
231 (Giraldeau and Ydenberg 1987), 50 m is a typical nearest-neighbour distance (Krebs 1971), and  
232 neighbour-stranger discrimination is typically strongest near the territorial border (Falls and Brooks  
233 1975; Stoddard et al. 1991). There is an inevitable trade-off between the advantages of our approach of  
234 broadcasting playbacks from a standard amplitude and distance from the nestbox, and those of

235 estimating males' actual territorial boundaries and placing the speaker at each male's estimated  
236 territorial edge. Because we used a fixed playback distance, our playbacks may have been more salient  
237 to some individuals than others, depending on whether the standard 25 m playback distance was or was  
238 not within their territory. However, although great tits differ in their response to playbacks well outside  
239 of their territory [10 m beyond the boundary] and those very close to the centre of their territory [20-30  
240 m within the boundary] (Peake et al. 2001), our setup was unlikely to have corresponded to this  
241 situation, and to our knowledge no study has examined whether great tits are capable of discriminating  
242 between songs coming from just inside versus just outside territorial boundaries. In contrast, it is well  
243 established that song intensity affects the aggressive response of songbirds, including great tits (Brumm  
244 and Ritschard 2011; Ritschard et al. 2012; Luther et al. 2016). Furthermore, song amplitude is likely to  
245 play a role in the speed of dear enemy learning (Bee 2001). We therefore used a fixed playback distance  
246 so that song amplitude could be standardized. The specific location of the playback was chosen in a  
247 randomized direction, with the constraint that playbacks were only performed from areas the  
248 experimenter could access, and that did not overlap with the territory of another male great tit.



249

250 **Fig. 1** (a) Timeline of the playback experimental design. We broadcast the neighbour stimulus ('NS') for  
251 five minutes per trial (number in each box corresponds to the trial number), for a total of three trials per  
252 day with approximately one hour between trials. This procedure was repeated for three consecutive  
253 days. On the third day, immediately following the final neighbour playback (NS 9), we broadcast a  
254 different song from a different location ('SS': stranger stimulus, a test of stimulus specificity, in other  
255 words that males that had reduced their response to the neighbour retain the capability of an aggressive  
256 response towards strangers). In 2017, the entire procedure was repeated with different stimuli after a  
257 period of ten days to test the repeatability of dear enemy behaviour. (b) Exemplar playback stimulus.  
258 The spectrogram shows a single great tit song that was used to build one of the playback stimuli. (c) a  
259 second exemplar stimulus, taken from a different bird, illustrating the acoustic variation in great tit  
260 songs. An example playback experiment could use the song in (b) for the neighbour stimulus and that in  
261 (c) for the stranger stimulus. Note that the spectrograms do not illustrate the equalization of playback  
262 amplitude that was used for the trials

263 On the third day, immediately after the response was recorded to the ninth exposure of the subject to  
264 the neighbour stimulus, we broadcast a different song stimulus from a different location (still 25 m away  
265 from the nestbox, and at a 90-degree angle or greater, with respect to the nest box, from the location of  
266 the neighbour playbacks). The aim was to compare the response to this new stimulus, simulating a new  
267 stranger individual (henceforth, the “stranger” stimulus), to the original playback stimulus to which we  
268 hypothesized the subject would have developed some familiarity towards. This is an essential step for  
269 demonstrating neighbour-stranger discrimination in territorial systems, in which individuals reduce their  
270 response to familiar neighbours, but maintain a heightened response to an unfamiliar stranger (Bee et  
271 al. 2016). In other words, the stranger playback was used to demonstrate that the decline in aggressive  
272 response observed across the trials is specific to the neighbour’s song. We performed the stranger  
273 playback immediately after recording the response to the last neighbour playback for logistical reasons  
274 and because doing so is a more conservative test of neighbour-stranger discrimination than if we had  
275 delayed the stranger playback by some interval. If an individual was not responsive to its neighbour but  
276 then immediately responded to the stranger playback, this is a strong test of the ability to discriminate  
277 between the two, whereas any delay between the playbacks increases the chance that any generalized  
278 habituation of the aggressive response would decline, potentially leading to misinterpretation of the  
279 data. Although it is possible that birds could have mounted an increased aggressive response during the  
280 stranger playback session not because they were responding to what they perceived as a stranger but  
281 rather because it was a novel situation in that the playback occurred a few minutes, rather than an hour,  
282 after the previous playback, we consider this interpretation unlikely because for this to be the case  
283 either birds would have had to learn the number of daily playbacks or the time interval between them,  
284 or would have had to interpret the playback as a different song type of the neighbour, which is unlikely  
285 because great tits are capable of learning individual voice characteristics and then discriminating among

286 them even based on songs they had never heard before (Weary and Krebs 1992) and therefore should  
287 not have mistaken our stranger stimulus for another song of the neighbour.

288

289 We justify our design of using both a different location and song for the stranger stimulus, because the  
290 aim of our experiment was not to identify the specific criteria used by individuals to discriminate  
291 neighbours and strangers, i.e., whether discrimination was based on these individuals' song  
292 characteristics or location, but rather to determine the consequences of individual differences in  
293 tendency to discriminate. Therefore, we used a playback design that increased the opportunities for  
294 discrimination between our stimuli by varying both location and song, which is also the most likely  
295 scenario for natural neighbour-stranger discrimination because the neighbour would not normally move  
296 to a different territory and the stranger would not normally sing from the exact spot that the neighbour  
297 was just singing in. We acknowledge that our design does not separate the effects of location and song  
298 type by including controls for each. This would not have been feasible given the longitudinal design and  
299 limited breeding window in this wild system. Furthermore, although we cannot rule out that subjects  
300 interpreted a song type recorded from a different bird and broadcast from a different location as in fact  
301 still coming from the original simulated neighbour, as discussed above, great tits discriminate among  
302 individual voice characteristics (Weary and Krebs 1992). Therefore, we interpret their responses in the  
303 final playback as responses to a simulated stranger, but note that, even under dear enemy relationships,  
304 individuals may also respond aggressively to neighbours when they display from a new location  
305 (Brindley 1991; Husak and Fox 2003; Lovell and Lein 2005; Dalton et al. 2020).

306

307 In 2017 only, we repeated this three-day procedure with 20 individuals ten days after their final trial  
308 from the first round of playbacks. The aim of this repetition was to investigate whether the expression  
309 of dear enemy behaviour was repeatable, which would indicate intrinsic differences among individuals

310 (Bell et al. 2009). Therefore, we performed playbacks as above, but with a different song stimulus from a  
311 different location, simulating a different new neighbour establishing a territory. A different stranger  
312 stimulus was also used in these repeated trials, and the male was given the alternative rate treatment to  
313 that which it had been exposed during the first round of playbacks.

314

315 Playbacks were performed between 0800h and 1540h; each male was tested at approximately the same  
316 time on each of the three days of the experiment. Playbacks occurred during the early stages of  
317 breeding for most birds – between late nest building and egg laying. Due to logistical constraints of  
318 running experiments across multiple field sites with respect to the timing of nest checks, seven  
319 individuals were tested after the last egg was laid at the nest, including three individuals for which  
320 incubation was already started at the nest (the latest start date of the first repetition of the playback  
321 trials was 4 days into incubation). To control for the timing of the playback with respect to the breeding  
322 cycle (Petrinovich et al. 1976; Mace 1987; Jin et al. 2021), we included the date of the first playback trial  
323 relative to the first egg date as a variable in analyses (see below).

324

### 325 *Playback procedure*

326

327 During each playback a single observer was positioned in cover near the playback speaker to monitor  
328 the male's behaviour, noting the distance between the bird and the speaker, and making audio  
329 recordings of any songs using Marantz PMD 660 or PMD 661 audio recorders with Sennheiser ME67  
330 directional microphones (16 bit, 44.1 kHz sampling rate). We did our best to avoid being observed by the  
331 birds during the playback; we consider it unlikely that our presence affected the results because these  
332 experiments took place in areas close to busy walking trails and birds were likely habituated to the  
333 presence of humans. All playbacks took place in locations where a male was known to occupy a territory

334 because on the days prior to the playbacks it was observed singing near the nestbox and there was  
335 evidence of nest building activity. Males were usually visually or acoustically located prior to the start of  
336 the playback, and if not, most were sighted during the playback. This was not always possible, however,  
337 and we assume that these males initially unseen were within hearing distance of the stimulus during the  
338 playback. This was reasonable because males spend the great majority of their time on their territories  
339 and when they do leave their territories they only move short distances (Firth et al. 2018); at such  
340 distances our playback stimulus amplitude would remain well above the species' masked hearing  
341 threshold (Langemann et al. 1998). Nevertheless, it is possible that we did not detect some response  
342 vocalizations from birds that were located far from the recorder, although signal to noise ratios of great  
343 tit song remain high at least 60 m from the source (Blumenrath and Dabelsteen 2004; Mockford et al.  
344 2011). Joint territory defence by two individuals in response to the playback was not observed in this  
345 study, possibly due to the low density of individuals at our study sites. It was not possible to record data  
346 blind because our study involved focal animals in the field.

347

#### 348 *Response variables*

349

350 We noted the closest approach of the male to the playback speaker, in categories of 5 m (Nelson and  
351 Soha 2004). Subjects were not always located at the nest box at the start of the playback, so values  
352 greater than 25 m were possible. Individuals that did not respond at all were given a value of "None" for  
353 closest approach, which in the ordinal analyses described below was considered the greatest distance  
354 (whereas closest approaches from 0-5 m were considered the shortest distance, with successive  
355 distance categories ranked according to their distance). From the audio recordings we counted the  
356 number of songs produced by the male during the playback. We considered males to have responded to  
357 the playback if they sang at any point during the stimulus broadcast, or made any movement towards



358 the playback speaker, and to have not responded if they did neither of those. The final dataset included  
359 51 individuals; data from the first trial recording for one bird included in this total were lost because of a  
360 faulty microphone cable.

361

### 362 *Criterion for dear enemy behaviour*

363

364 The typical method for demonstrating the dear enemy effect is to present individuals, in a single  
365 playback session, with the signals of an actual established neighbour, followed by a single playback  
366 session presenting the signals of an individual that the subject could not have interacted with previously  
367 (Brunton et al. 2008; Wei et al. 2011; Battiston et al. 2015). The dear enemy effect is inferred when  
368 individuals have a reduced response to the neighbour stimulus compared to the stranger stimulus. In  
369 our protocol we simulated the establishment of a new neighbour through a series of playbacks, which  
370 essentially served as training sessions to give the subject the opportunity to learn to recognize its  
371 neighbour. Therefore, to test whether or not the subject was indeed exhibiting dear enemy behaviour at  
372 the end of the necessarily fixed number of trials, we used the typical criterion for testing the dear enemy  
373 effect: comparison of the response to a final neighbour playback and a stranger playback. Our criterion  
374 (hereafter referred to as the 'standard criterion') that the subject was expressing dear enemy behaviour  
375 was that it did not respond in the final (ninth) playback of the simulated neighbour, but then did  
376 respond to the subsequent (tenth) playback of a simulated stranger.

377

378 Although our binary criterion should theoretically identify individuals that were expressing dear enemy  
379 behaviour towards the simulated neighbour, it has its limitations, so we explored additional measures of  
380 an individual's change in response towards its neighbour over time. First, in some cases individuals  
381 responded to neither the final neighbour playback nor the stranger playback (N = 21). These results are

382 difficult to interpret because they may indicate a general loss of motivation to defend the territory  
383 rather than a failure to discriminate neighbours and strangers. We therefore repeated all analyses,  
384 defining dear enemy behaviour as above, but only including those birds that responded to the stranger  
385 stimulus (referred to as the 'standard criterion without non-responders'; N = 30 of 51 birds meeting this  
386 criterion; no individual failed to respond to the stranger playback after responding to the final neighbour  
387 playback). Second, for each individual, we extracted slope parameters from a logistic regression of the  
388 binary response variable on trial number (not including the stranger playback; referred to as the  
389 'response slope criterion'), and a linear regression of the number of songs on trial number (referred to  
390 as the 'song slope criterion'). The aim was to obtain a more quantitative estimate of the change in  
391 response across trials that may reveal more variation than our binary criterion. If individuals have  
392 developed dear enemy behaviour towards the newly established neighbour, these values would be  
393 expected to be negative, indicating a decline in response across trials. However, a decline in response to  
394 a neighbour is not sufficient to demonstrate the dear enemy effect, because individuals must continue  
395 to respond to strangers. Therefore, we only included individuals that responded to the stranger  
396 playback for this second set of analyses (N = 30).

397

### 398 *Breeding data*

399

400 Breeding data were obtained as part of standard monitoring protocols for the project (O'Shea et al.  
401 2018). We recorded the date when the first egg was laid, the total clutch size, date of hatching and  
402 number of fledglings. The identity of the subject male sometimes could be determined by identification  
403 of unique colour rings if the male had already been captured prior to the experiment. Some males were  
404 also identified using RFID-equipped nestbox entrance doors, which could read the unique passive  
405 integrated transponder tag placed on the leg of previously captured males. The age (first year juvenile or

406 adult) of previously captured males was determined from capture records. Males could also be  
407 identified when breeding adults were caught at the nest for ringing, ageing (as either first year juveniles  
408 or adults), and measurements, 10-12 days after the eggs hatched. Fifteen subjects were not identified  
409 because the nest was abandoned prior to trapping (N=1 before eggs laid, N=8 before eggs hatched, N=5  
410 after eggs hatched), or the male could not be caught (N=1). However, our analyses do not rely on  
411 knowing the specific identity of the subject, and we can safely assume that no male was recorded in the  
412 study more than once based on the timing and distribution of boxes at which playbacks were carried out  
413 across the eight sites. Breeding densities are low at our sites and in cases where males could not be  
414 identified by colour-rings we nevertheless consider it highly unlikely that more than one individual  
415 responded to the playback on different trials. Chicks were weighed at day 15, and we determined the  
416 number of fledglings by inspecting the nest for any dead chicks after the breeding attempt was  
417 complete.

418

#### 419 *Paternity analysis*

420

421 Estimates of male reproductive fitness can be strongly influenced by extra-pair paternity (EPP) (Webster  
422 et al. 1995). Although rates of EPP are relatively low in great tits (van Oers et al. 2008; Patrick et al.  
423 2012), they could have altered the relationship between dear enemy behaviour and reproductive  
424 fitness, particularly as paternity loss is one of the potential costs of territorial intrusions, and neighbours  
425 and strangers may differ in the threat they pose to paternity (Schlicht et al. 2015). EPP levels may also  
426 influence selection on males to cooperate via dear enemy effects (Eliassen and Jørgensen 2014). We  
427 therefore analyzed males' reproductive success using metrics that excluded any offspring that were  
428 identified in a paternity analysis as being extra-pair offspring (note that we did not attempt to quantify  
429 males' success at obtaining extra-pair matings at other nests because the small size and fragmented

430 nature of our study sites prevented us from confidently assessing a male's reproductive output away  
431 from his own nest). This is the appropriate method to analyse fitness, but we were also interested in the  
432 consequences of dear enemy behaviour on parental care behaviour. Therefore, we performed an  
433 additional set of analyses on the reproductive success variables in which both within-pair and extra-pair  
434 young were included, and present these in the supplement (results were not qualitatively affected by  
435 whether or not we excluded extra-pair young).

436

437 DNA was obtained from feathers taken from breeding pairs and offspring on their respective dates of  
438 capture and ringing. DNA extraction was performed using the protocol of the E.Z.N.A. Tissue DNA Kit  
439 (Omega Bio-Tek, Norcross, GA, USA), with the exception of the use of 80  $\mu$ L elution buffer on a single  
440 elution step. Samples were genotyped at eight microsatellite loci, selected based on previously observed  
441 variability and utility, as well as potential for multiplexing in a single reaction (Pma69u (k=7 alleles)  
442 (Kawano 2003); PmaD22 (k=20), PmaCan1 (k=15), PmaGAn30 (k=5), PmaC25 (k=19), PmaTAGAn86  
443 (k=19), PmaTGAN33 (k=17) and PmaTGAN45 (k=11) (Saladin et al. 2003)). Multiplex PCR was performed  
444 in a 3.5  $\mu$ l total volume, including 1  $\mu$ l of DNA extract, and 1.75  $\mu$ l of 2x Top-Bio™ Plain Combi PP  
445 Mastermix, with a concentration of 0.03  $\mu$ M for the Pma69U, PmaCan1, PmaGAn30 and PmaTAGAn86  
446 primers and 0.06  $\mu$ M for the PmaC25, PmaD22, PmaTGAN33 and PmaTGAN45 primers. The PCR was  
447 programmed with an initial denaturation at 95°C (15 min) followed by five cycles of 94°C (30 s), 55°C (90  
448 s), 72°C (60 s), then 27 cycles at 94°C (30 s), 57°C (90 s), 72°C (60 s), followed by an elongation step at  
449 60°C for 30 min. The PCR products were diluted in 14  $\mu$ L nuclease free water; and run on an Applied  
450 Biosystems ABI3500xl DNA analyser using POP-7 polymer with GeneScan™ 600 LIZ™ Dye Size Standard  
451 v2.0 (ThermoFisher Scientific). We used GeneMarker version 2.7.0 software (SoftGenetics, Pennsylvania,  
452 USA) to determine allele sizes.

453

454 Paternity was assigned using CERVUS version 3.0.7 software (Kalinowski et al. 2007) using 10,000 cycles,  
455 94 candidate fathers, a 0.02% error rate, two candidate parents and 93% of loci typed as simulation  
456 parameters. Only individuals that were successfully genotyped at five or more loci were included in  
457 paternity analyses. Individuals were determined to be within-pair offspring if all loci matched those of  
458 the social father and social mother combination, or if there was a mismatch at only one of the loci but  
459 the social father was identified as the most likely father using critical trio LOD scores returned by the  
460 program. Offspring that did not meet these criteria were categorized as extra-pair offspring. We  
461 assumed that offspring whose paternity was not determined (9 of 96 fledged offspring and 13 of 111  
462 weighed offspring were of unknown paternity; two offspring fledged but were not weighed or analysed  
463 for paternity because they fledged on the day of weighing) were within-pair offspring. The combined  
464 exclusion probability for all eight microsatellites was >99.99%. Two of our loci significantly deviated from  
465 Hardy-Weinberg equilibrium when the genotypes of all individuals in the analysis were included  
466 (PmaC25:  $\chi^2 = 40.98$ , df = 15,  $p < 0.001$ , PmaD22:  $\chi^2 = 33.87$ , df = 15,  $p = 0.004$ ). This was likely due to  
467 the family structure of the data.

468

#### 469 *Data analysis*

470

471 Except for the analyses of repeatability (see below), all analyses were performed only on the first  
472 repetition of the playback trials (i.e., we excluded data from the second repetition of the three-day  
473 procedure that was performed in 2017 only). We address the following questions in our analyses:

474

475 1. Does the response to the neighbour playback decrease over time? We tested whether males reduced  
476 their aggressiveness as they became more exposed to the songs of another male using three different  
477 variables, all of which have been demonstrated to be related to the aggressive response in great tits in

478 previous studies (McGregor and Avery 1986; Doutrelant et al. 2000; Amy et al. 2010; Snijders et al.  
479 2017): “response”, i.e. whether the male responded at all by singing or approaching (binary), closest  
480 approach (ordinal categorical), and number of songs during individual trials. In all cases the trial number  
481 (1-9) and stimulus rate treatment (low or high) were entered as fixed effects, and individual identity as a  
482 random effect. Response was modelled using a binomial generalized linear mixed model using the glmer  
483 function in the lme4 version 1.1-23 package (Bates et al. 2015) in R 4.0.2 software (R Development Core  
484 Team 2021). Approach category was modelled using a cumulative link mixed model to account for the  
485 ordinal nature of the dependent variable using the clmm function in the ordinal 2019.12-10 package  
486 (Christensen 2019). Number of songs was modelled as a poisson variable using the glmmTMB function  
487 of the glmmTMB 1.0.2.1 package (Brooks et al. 2017), which accounts for zero inflation in the dataset.

488

489 2. Is there a difference in the response to the stranger playback compared to the final (ninth) familiar  
490 neighbour playback? If there was a decrement in aggression in the analyses above, the next step to  
491 demonstrate dear enemy behaviour is to show that this decrement is specific to the neighbour stimulus.  
492 Therefore, individuals were predicted to respond more strongly to the stranger playback than to the  
493 final neighbour playback. We tested the same variables as above, using the same analyses but with the  
494 trial variable a factor with two levels: final neighbour or stranger playback trial.

495

496 3. Is the tendency for individuals to form a dear enemy relationship within the timeframe of our  
497 playback design repeatable? We estimated the repeatability of neighbour-stranger discrimination using  
498 the rptR package (Nakagawa and Schielzeth 2010) with the repetition (first or second) and stimulus rate  
499 treatment as fixed factors, individual as a random factor and whether the individual did or did not meet  
500 the standard criterion (i.e., responded to the stranger but not the neighbour stimulus) as a binary  
501 dependent variable. One individual was removed from this analysis because it did not respond during

502 any trial in the second repetition. Repeatabilities of the response and song slope measures were  
503 analysed similarly, but with the dependent variable modelled as Gaussian.

504

505 We examined the context-dependence of dear enemy behaviour using separate models for each of the  
506 four different methods of quantifying dear enemy behaviour (see *Criterion for dear enemy recognition*,  
507 above). We used generalized linear models for the standard criterion and standard criterion without  
508 non-responders, and linear models for the response slope and song slope. In all cases, we tested for  
509 effects of year (2017 or 2018), date of the first playback, date of the first playback minus the date the  
510 first egg was laid (to account for variation in dear enemy behaviour across the breeding cycle (Jin et al.  
511 2021)), stimulus repetition rate (low or high), and the average number of songs the subject produced  
512 across the nine neighbour playbacks, as an estimate of its overall 'aggressiveness'. We performed  
513 separate models for male age, with model structure as above but age (first year or adult) as the only  
514 factor, because age was only known for a subset of the birds.

515

516 4. Is there evidence for a difference in reproductive fitness between individuals that did or did not  
517 express dear enemy behaviour? We ran separate models for each of four different metrics of  
518 reproductive success, controlling for paternity, and each of the four methods of quantifying dear enemy  
519 behaviour (see *Criterion for dear enemy recognition*, above). For these analyses, we excluded data from  
520 three males from one of the sites (Dunderrow, see Table S1) in 2018 because of widespread nest  
521 predation. Although predation is certainly a component of reproductive success, in this site almost every  
522 nest was completely predated by stoats, *Mustela erminea*, and therefore we consider that there could  
523 be no relationship between the male phenotypic characteristics under study and the survival of  
524 offspring in this site with unusually high predation, rendering reproductive measures of these individuals  
525 meaningless in the context of our hypotheses.

526  
527 In all reproductive success models we included the metric of dear enemy behaviour, as defined above,  
528 as a fixed factor. Initial models also included the date the first egg was laid in the clutch, with the first of  
529 March as day 1, as well as the date of the first playback trial relative to the first egg date, but neither of  
530 these variables ever explained variation in reproductive success and so were excluded from the final  
531 models (similar results on the lack of effects of these variables on reproductive success were found by  
532 (O'Shea et al. 2018)). Four measures of reproductive success were analysed as follows: A) Clutch size  
533 was modelled as a Poisson variable in a generalized linear model. For one subject, no eggs were laid at  
534 the nestbox, and it was therefore excluded from all analyses of reproductive success; B) Number of  
535 within-pair fledglings was a Poisson variable, but there were a large number of zero values. We  
536 therefore modelled it with a glmmTMB model that accounts for zero inflation. In addition, because of  
537 the large number of zero values, we ran a model with the binary dependent variable of whether or not  
538 any offspring were fledged from the nest to compare males with successful versus unsuccessful nests; C)  
539 Average mass of within-pair offspring on day 15. Offspring biomass is an important determinant of  
540 fitness (Tinbergen and Boerlijst 1990), although this variable excludes the large number of subjects  
541 (N=18) whose nests failed entirely before day 15 (we had no evidence that these failures were caused by  
542 predation (e.g. broken eggs or predated remains), and instead were likely due to either parental  
543 abandonment or natural death of all offspring; note that the latter two causes are not readily  
544 distinguished), which of course is a severe fitness cost. We entered average offspring mass as the  
545 dependent variable in a linear model with an additional factor of brood size (including both within- and  
546 extra-pair offspring); D) The actual mass of each individual within-pair offspring. This analysis also  
547 excludes failed nests but may reveal important variation in parental investment among those nests that  
548 did survive. Individual mass was entered as a Gaussian variable in a linear mixed model, with brood size  
549 as an additional factor and nest as a random effect.



550

551 Initial models with site included as a random effect could not be run because of singularity issues,  
552 because there were few samples from most sites (see Table S1). For the same reason, we did not  
553 perform a formal analysis of reproductive success by site, but there were no obvious qualitative  
554 differences in these variables between the four sites with the largest numbers of individuals tested  
555 (Table S1).

556

557 We then repeated the above analyses including all nestlings (i.e., both within-pair and extra-pair) to  
558 determine if there was evidence for any benefit in the social nest of the tendency to perform dear  
559 enemy behaviour. We did not reanalyse clutch size because the analyses above also included all eggs,  
560 both within- and extra-pair, because we did not determine paternity for all eggs.

561

562 5. Finally, we tested for a relationship between dear enemy behaviour and extra-pair paternity using the  
563 proportion of extra-pair young at the nest as the dependent variable (binomial; general linear model),  
564 and, in separate models, each measure of dear enemy behaviour as a factor.

565 RESULTS

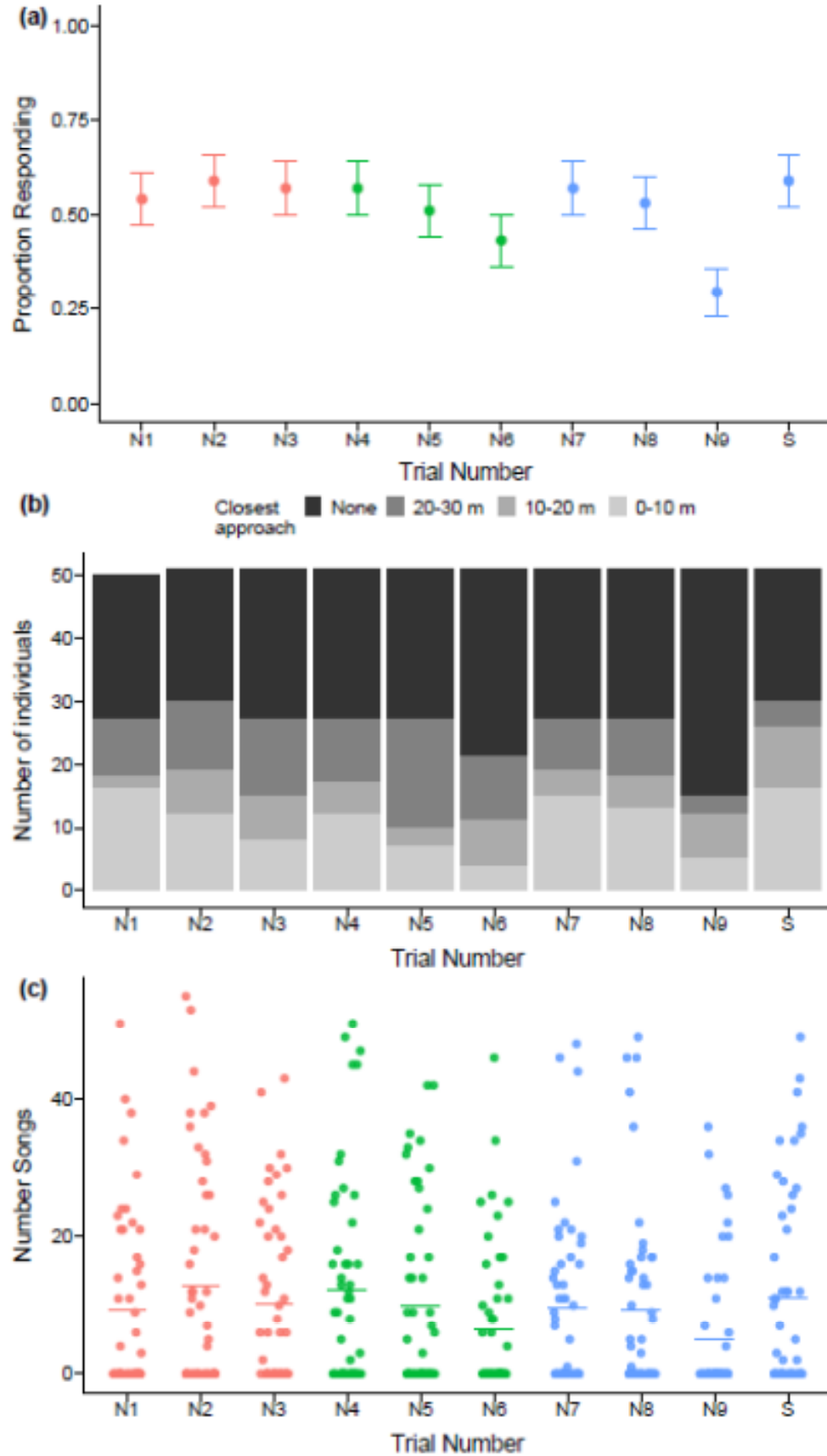
566

567 *Change in response to the neighbour playback*

568

569 The likelihood of a response (singing and/or moving towards the speaker) significantly decreased across  
570 the neighbour playback trials (Table 1; Fig. 2a). The pattern of responses shows an initial slight increase  
571 in the likelihood of responding over the first few trials, and then larger decreases especially in the final  
572 trials of the day. Closest approach was significantly greater on later trials such that individuals were  
573 more likely to make a close approach to the speaker on earlier trials, and approached but stayed further  
574 away or did not approach at all on later trials (Table 1; Fig. 2b). Likewise, the number of songs produced  
575 by males during the playback decreased across trials (Table 1; Fig. 2c). There was no effect of stimulus  
576 rate on response or closest approach, but there was a non-significant trend for an effect on the number  
577 of songs, with males giving more songs in response to stimuli presented at the higher rate (Table 1).

578



580 **Fig. 2** Response across trials. (a) The proportion ( $\pm$ SE) of individuals ( $N = 51$  for all trials except  $N = 50$  for  
581  $N1$ ; see Methods) that responded by either singing or approaching the playback speaker in each of the  
582 nine neighbour playback trials (labelled  $N1-N9$ ) and on the stranger playback trial. Colours correspond to  
583 the day that the playback was performed (red = day 1, green = day 2, blue = day 3). (b) The closest  
584 approach, in categories of 10 m (note that in the statistical analyses we used categories of 5 m, but for  
585 ease of visualization we use broader categories here). None corresponds to trials in which the bird did  
586 not move at all towards the playback speaker. (c) The number of songs produced by males during the  
587 playback trial. Dots represent an individual's response to that trial (points have been jittered along the x-  
588 axis and rendered partially transparent for ease of interpretation). Horizontal lines represent mean  
589 values.

590 **Table 1** Tests of change in response to neighbour playback across trials. Output is from a generalized  
591 linear mixed model for response (binary, yes or no), a cumulative link mixed model for closest approach  
592 (distances were placed into ordinal categories), and a zero-inflated glmm for number of songs (Poisson;  
593 the coefficients are for the conditional model output). The reference category for stimulus rate is the  
594 low rate (estimate = 0). Trial number was entered as a numerical variable, with values from one (first  
595 trial with neighbour stimulus) to nine (last trial with neighbour stimulus).  $N = 51$  individuals  
596  
597

Variable	Factor	Estimate (SE)	z	P
Response	Intercept	0.53 (0.27)		
	Trial number	-0.10 (0.04)	-2.52	0.01
	Rate (high)	0.04 (0.28)	0.13	0.89
Closest approach	Trial number	0.11 (0.04)	3.10	0.002
	Rate (high)	-0.01 (0.30)	-0.03	0.97
Number of songs	Intercept	2.91 (0.09)		
	Trial number	-0.04 (0.01)	-5.88	<0.001
	Rate (high)	0.23 (0.12)	1.89	0.058

598

599

600 *Stimulus specificity of response to neighbour playback*

601

602 Although twice as many individuals responded to the stranger playback compared to the (immediately  
603 preceding) final neighbour playback, this difference was not significant (Fig. 2A; Table 2). However, there  
604 was a significant difference in both the closest approach to the speaker and in the number of songs  
605 between the final neighbour playback and the stranger playback: individuals approached closer and sang  
606 more songs in response to the stranger playback (Fig. 2b, c; Table 2). Thus, the decline in the response  
607 was specific to the neighbour's song (stimulus), which suggests dear enemy discrimination rather than a  
608 general decrease in aggression. Stimulus rate did not affect the responses when only these two trials  
609 were considered (Table 2).

610

611 **Table 2** The effects of stimulus specificity and stimulus rate on response to neighbour playback. Output  
612 is from models as in Table 1, but now only including the response to the final neighbour playback and  
613 the stranger playback; estimate shown for the stranger trial (10) and the reference category (estimate =  
614 0) is the final neighbour playback (trial 9). The parameter estimate for the high stimulus rate is shown  
615 and the reference category is the low rate.  $N = 51$  individuals

616

617

Dependent variable	Factor	Estimate (SE)	z	P
Response	Intercept	-2.54 (2.51)		
	Stimulus (stranger)	3.59 (3.33)	1.08	0.28
	Stimulus rate (high)	-0.12 (1.42)	-0.08	0.94
Closest approach	Stimulus (stranger)	-2.09 (0.56)	-3.73	<0.001
	Stimulus rate (high)	0.13 (0.79)	0.17	0.87
Number of songs	Intercept	-0.04 (0.74)		
	Stimulus (stranger)	0.30 (0.08)	3.56	<0.001
	Stimulus rate (high)	0.04 (0.92)	0.04	0.97

618

619

620 *Repeatability and context dependence of dear enemy behaviour*

621  
622 Based on our standard criterion of no response to the final neighbour playback followed by a response  
623 to the stranger playback, 15 of 51 individuals exhibited dear enemy behaviour towards their simulated  
624 neighbour after the nine playbacks (Table S2; 15 of 30 when non-responders were removed i.e. standard  
625 criterion without non-responders, see Methods; these results refer only to the first set of playbacks, and  
626 do not include the second set of playbacks that were performed in 2017). There was a trend for  
627 significant repeatability in the standard criterion for dear enemy behaviour, with a moderate  
628 repeatability coefficient ( $N = 19$  individuals tested twice;  $R = 0.44$ ,  $P = 0.074$ ). Five of six individuals that  
629 showed dear enemy behaviour in the first set of playbacks also did so in the second, and six of 13  
630 individuals that did not show dear enemy behaviour in the first set of playbacks also did not show it in  
631 the second set. There were insufficient numbers of individuals tested twice and responding to the  
632 stranger playback to allow for estimating the repeatability of the slope for response or number of songs  
633 across trials.

634  
635 Whether an individual met the standard criterion for dear enemy behaviour (whether including or  
636 excluding non-responders) did not depend on the date of testing, the date relative to the day on which  
637 the first egg was laid, the year, the average number of songs produced by the subject across the  
638 neighbour playbacks, or the stimulus rate (Table S3). These variables also did not affect the slope of the  
639 response or number of songs across trials (Table S3). There was also no effect of age (first year versus  
640 older) on meeting the standard criterion for dear enemy behaviour (Estimate of effect being older than  
641 first year  $\pm$  SE =  $-1.29 \pm 0.88$ ,  $z = -1.46$ ,  $P = 0.15$ ;  $N = 33$  individuals of known age; standard criterion  
642 without non-responders:  $-0.47 \pm 0.97$ ,  $z = -0.48$ ,  $P = 0.63$ ,  $N = 18$ ). However, there was an effect of age  
643 on the slope of number of songs across trials, with older birds having a less negative slope than first year



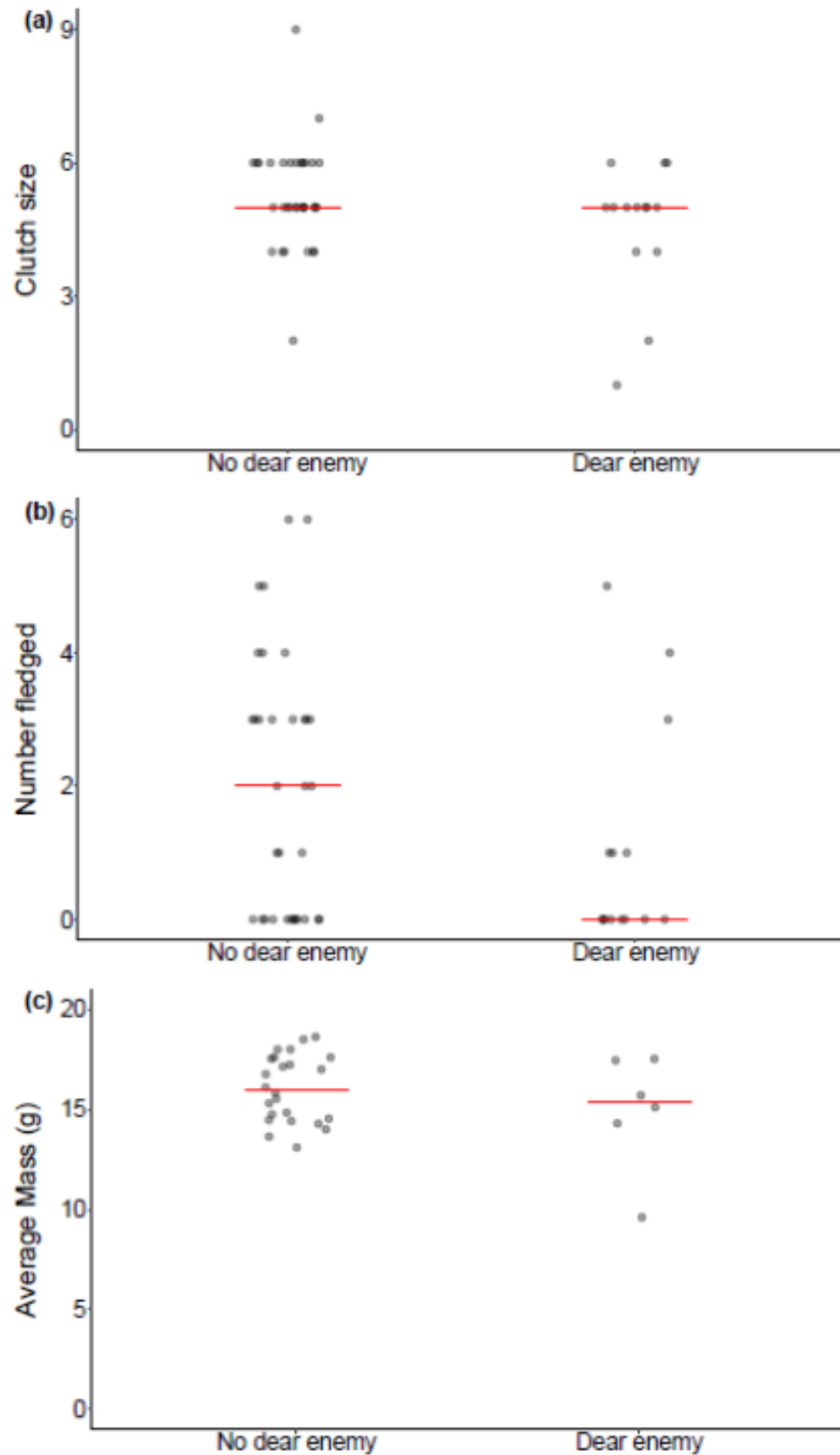
644 birds (Estimate =  $2.96 \pm 0.83$ ,  $t = 3.57$ ,  $P = 0.003$ ;  $N = 17$  individuals of known age) and also on the slope  
645 of responses across trials (Estimate =  $0.07 \pm 0.03$ ,  $t = 2.33$ ,  $P = 0.03$ ;  $N = 17$ ).

646

647 *Reproductive success and dear enemy behaviour*

648

649 There was no effect of whether an individual exhibited dear enemy behaviour (standard criterion) on  
650 the number of eggs laid in its nest (Fig. 3a; Table S4). Sixteen offspring were identified as extra-pair  
651 young and were excluded from the analyses of number of offspring fledged and offspring mass. There  
652 was also no effect of whether an individual exhibited dear enemy behaviour (standard criterion) on the  
653 number of within-pair offspring that fledged (Fig. 3b; Table S4), or on the binary variable of whether or  
654 not any offspring were fledged (Table S4). For the limited set of individuals that fledged young, there  
655 was no effect of whether it had met the standard criterion for dear enemy behaviour on the average  
656 mass of its within-pair offspring (Fig. 3c; Table S4) or on the individual mass of within-pair offspring  
657 (Table S4). When the standard criterion without non-responders, the slope of responses, or the slope of  
658 the number of songs across trials was used as the response variable, there were again no significant  
659 effects on any of the reproductive success measures (Table S4). When we repeated the above analyses  
660 but this time including data from both within-pair and extra-pair young, we again found no relationship  
661 between dear enemy behaviour and any measure of reproductive success (Table S5). Finally, there was  
662 no difference between individuals that did or did not show dear enemy behaviour (standard criterion) in  
663 the proportion of fledglings that were extrapair (Estimate =  $0.20 \pm 0.71$ ,  $P = 0.78$ ,  $N = 29$  nests).



665 **Fig. 3** Relationship between whether the individual met the standard criterion (see Methods) for  
666 exhibiting the dear enemy effect (“Dear enemy”) or not (“No dear enemy”) and different measures of  
667 reproductive success. Each dot represents the value for an individual nest (points jittered along the x-  
668 axis and rendered partially transparent); red horizontal line represents the median. (a) Clutch size, (b)  
669 Number of within-pair offspring successfully fledged, (c) Average mass of within-pair offspring at day 15  
670 post hatch (not including nests for which no offspring survived to day 15).  $N = 47$  individuals in each  
671 graph, except for (c) where  $N = 30$   
672

673 DISCUSSION

674

675 Male great tits in our study populations exhibited an overall decline in song response and approach  
676 towards the neighbour playback stimulus across repeated presentations, consistent with reduced  
677 aggression towards an increasingly familiar individual. This reduced aggression was stimulus-specific  
678 because in the stranger playback, simulating a different individual, subjects reverted to a strong  
679 response to the playback. This is consistent with dear enemy behaviour because at the end of the trials,  
680 individuals were less aggressive towards the neighbour than the stranger. Our experiments show that  
681 neighbour-stranger discrimination can arise and be expressed in only three days, although this was not  
682 the case for all individuals. Against predictions, there was no fitness benefit for individuals that exhibited  
683 dear enemy behaviour, and no reproductive benefit of any kind that we could detect. Below we discuss  
684 these results in the context of territorial aggression and the evolution of neighbour-stranger  
685 discrimination.

686

687 *Learning mechanisms and individual variation*

688

689 Although complex cognitive mechanisms such as ‘true’ individual recognition (Tibbetts and Dale 2007)  
690 are sometimes involved in dear enemy behaviour, and more complex associations between neighbours  
691 may arise, perhaps requiring long-term memory, such as coalitions or associations outside the breeding  
692 season (McGregor and Avery 1986; Grabowska-Zhang et al. 2012a; Firth and Sheldon 2016), in many  
693 species habituation learning of some characteristic of neighbours is a major contributor to the reduced  
694 aggression towards those individuals that is characteristic of the dear enemy effect (Petrinovich and  
695 Peeke 1973; Brooks and Falls 1975; Peeke 1984; Bee and Gerhardt 2001; Dong and Clayton 2009). We  
696 showed that at least some individuals distinguished simulated neighbours from strangers, and that the

697 pattern of response change across trials matches many of the characteristics of habituation (Thompson  
698 and Spencer 1966; Rankin et al. 2009).

699

700 First, the response to repeated playback of a simulated neighbour decreased across trials (Table 1).

701 Second, there was evidence for spontaneous recovery of the response across days, in which the  
702 response on the first trial of the day was generally greater than that of the last trial on the previous day  
703 (Fig. 2). A key characteristic of habituation is that over a series of recoveries and decrements,  
704 habituation is potentiated, with the response decrement becoming ever more pronounced (Thompson  
705 and Spencer 1966; Rankin et al. 2009). Although our nine testing sessions were conducted across just  
706 three days, comparisons of behaviour on day 2 and day 3 show that the response decrease was much  
707 greater on day 3, consistent with a potentiation of habituation effect. Note that the dear enemy effect  
708 does not necessarily require that aggression towards neighbours is eliminated entirely, and indeed  
709 increased responsiveness to neighbours at the beginning of the day seems to be common in birds  
710 (Briefer et al. 2008; Foote et al. 2008) and may serve to maintain the stability of the territorial boundary.

711 Third, the dual-process theory of habituation argues that in addition to the decrement in response  
712 caused by habituation, an independent process of sensitization results in an initial, but transient,  
713 increase in aggressive response (Groves and Thompson 1970; Petrinovich and Patterson 1982).

714 Consistent with sensitization, responses tended to be weaker on the first playback trial compared to the  
715 subsequent few trials. Importantly, the expression of habituation can be context-dependent through the  
716 formation of associations between the habituating stimulus (e.g. the neighbour playback song) and a  
717 context (e.g. the location at which the neighbour playback was performed) (Jordan et al. 2000; Uribe-  
718 Bahamonde et al. 2019); thus, although our experimental design did not involve independent  
719 manipulations of stimulus location and song type, the association between these two variables does not  
720 rule out a habituation mechanism for the stimulus-specific reduction in aggression we observed.

721  
722 Against habituation being the mechanism underlying the observed decline in response, habituation was  
723 not stronger at higher song repetition rate, as might have been expected. However, most effects of  
724 stimulation interval on habituation have been demonstrated based on variation in the intervals between  
725 successive playbacks (rather than between successive songs within a playback), which were  
726 approximately the same for the birds in our study, so this prediction may not apply (Groves and  
727 Thompson 1970; Thompson et al. 1973; Bee 2001). Taken together, our results suggest that habituation  
728 learning is one of the key mechanisms behind the initial stages of dear enemy behaviour in great tits,  
729 which was expected, given the general importance of habituation in territorial aggression in songbirds  
730 and its specific well-established role in dear enemy recognition (Peeke 1984; Ydenberg et al. 1988; Dong  
731 and Clayton 2009). Nevertheless, natural dear enemy relationships in these species almost certainly  
732 involve other cognitive mechanisms as well and elucidating the relative contributions of these  
733 mechanisms to individual variation in dear enemy behaviour is a worthy target of future research.  
734 Furthermore, it is possible that different individuals of the same species use different cognitive  
735 mechanisms for individual recognition, and this could have influenced their pattern of response and  
736 whether or not they exhibited dear enemy behaviour in this study (Gokcekus et al. 2021).

737  
738 Non-cognitive mechanisms could also explain the variation in dear enemy behaviour we observed.  
739 Differences in average aggressiveness can affect response to playback in great tits (Araya-Ajoy and  
740 Dingemanse 2014), and could have played a role, although we found no effect of the average number of  
741 songs in response to the neighbour playbacks (a plausible measure of aggressiveness) on whether  
742 subjects exhibited dear enemy behaviour. Variation in other personality traits such as explorativeness is  
743 also known to relate to variation in habituation speed in great tits (Rivera-Gutierrez et al. 2017) and  
744 could therefore have driven some of the variation observed in our study. Given that we did our

745 experiment in a wild population, males could have differed in experience that influenced their response  
746 to playbacks. Specifically, males varied in the extent to which they had already interacted with different  
747 territorial neighbours in the past. Great tits with more prior exposure to songs of many neighbours are  
748 slower to learn to recognize new neighbours (McGregor and Avery 1986), and indeed we found that  
749 older birds showed a slower decrement in response and number of songs across the trials than did first  
750 year birds, although this did not result in differences between the age groups in whether they differed in  
751 response to the final neighbour playback versus the stranger playback. Factors such as density and  
752 progress of the breeding season often explain variation in the dear enemy effect (Hyman 2005; Pratt  
753 and McLain 2006; Yoon et al. 2012), including in great tits (Jin et al. 2021). However, we found no  
754 evidence for this in our study: there was no effect of year, date, or date relative to the start of hatching  
755 on whether individuals expressed the dear enemy effect. Whatever the exact mechanisms involved, the  
756 individual repeatability in dear enemy behaviour we report indicates that we captured intrinsic  
757 differences among individuals in how they discriminated between familiar neighbours and strangers.

758  
759 We found behaviour consistent with the dear enemy effect because over time individuals responded  
760 less to the stimulus simulating the establishment of a new neighbour than to a stimulus that simulated  
761 an unknown stranger. It could be objected that subjects did not actually recognize the playback as a true  
762 neighbour, and the other as a different stranger bird, and that therefore the stimulus-specific response  
763 decrement we observed is not the same as the dear enemy effect. In the strict sense, even playback  
764 designs using songs of true neighbours do not necessarily overcome this objection, because even  
765 demonstrating a stimulus- and location-specific response to a true neighbour's songs does not give  
766 definitive evidence that this stimulus was recognized as the territorial neighbour, rather than being a  
767 stimulus that the individual had simply habituated to. We justify our approach and interpretation  
768 because 1) we were interested in individual variation in the cognitive processes involved in establishing

769 dear enemy relationships, which cannot be studied with established neighbours. Given the frequency of  
770 habituation as a mechanism for dear enemy recognition and the very rapid settlement of territorial  
771 relations and habituation to song in great tits (Krebs et al. 1981; Peeke 1984; Rivera-Gutierrez et al.  
772 2017), our design was appropriate. 2) Although no playback can ever replicate the interactions that take  
773 place between two birds, we replicated the essential features of territorial neighbours – an increasingly  
774 familiar song from the same location on an adjacent territory – and those of strangers – an unfamiliar  
775 song from a different location. Song familiarity and location are likely the two most important elements  
776 in dear enemy behaviour in great tits, and the behaviour we observed was consistent with the  
777 expression of the dear enemy effect. 3) Our simulated neighbour approach reduces some of the  
778 confounding effects associated with using playbacks of an established neighbour such as individual  
779 variation in experience with that neighbour (Falls et al. 1982; Grabowska-Zhang et al. 2012a).  
780 Nevertheless, additional studies of dear enemy behaviour in this species that examine its expression  
781 over longer time periods and incorporating additional stimulus dimensions and long-term observations  
782 of interacting individuals would be valuable.

783

#### 784 *Dear enemy recognition and fitness*

785

786 We hypothesized that if the dear enemy effect is adaptive because it reduces time spent in unnecessary  
787 aggressive interactions or leads to other beneficial interactions with neighbours (Getty 1987; Temeles  
788 1994), then individuals that reduce the aggression directed towards their neighbours more quickly  
789 would have higher reproductive benefits leading to increased reproductive fitness. There was good  
790 reason to expect these predictions to be met in our system because male great tits are known to trade  
791 off foraging and territory defence (Ydenberg 1984). We reiterate that our experiment was based on the  
792 premise that individual variation in the reduction in aggression to the neighbour stimulus and



793 subsequent response to the stranger stimulus served as a proxy for individual variation in the tendency  
794 to form dear enemy relationships in natural interactions, and it was the latter that we proposed to drive  
795 any fitness effects. Our hypothesis was not supported because there was no difference in clutch size,  
796 average biomass, or number of offspring that fledged between individuals that did or did not express  
797 the dear enemy effect. This was true in terms of the measure most closely related to male fitness (when  
798 extra-pair paternity was excluded) but it was also true for the overall reproductive success at the nest  
799 (when extra-pair young were included), for which detectable effects should be most apparent. In a field  
800 experiment of this nature on a species with a complex multi-stage reproductive strategy, inevitably  
801 many processes could explain this result, and we highlight those that we suggest particularly deserve  
802 attention in future research.

803  
804 First, ‘enemies may not always be dear’ (Muller and Manser 2007; Courvoisier et al. 2014; Moser-Purdy  
805 et al. 2017), and there may be costs associated with reducing aggression. For example it may lead to  
806 prospective individuals settling, leading to reduced territory size and quality (Getty 1989), or to reduced  
807 rates of provisioning offspring by the males (Sillett et al. 2004). Reduced aggression by males could have  
808 also led to the cost of their mates engaging in extrapair copulations with neighbours, though we found  
809 no evidence of this, nor did a previous study of song sparrows, *Melospiza melodia* (Krippel et al. 2017).  
810 We note, however, that reduced aggression could also have led to reduced extra-pair paternity if it  
811 facilitated mate guarding, though we also found no evidence for this. Second, the lack of any observed  
812 benefit to dear enemy behaviour could be because it traded off against other fitness-related behaviours.  
813 For instance, in great tits, a positive association between problem solving performance and both clutch  
814 size and number of fledglings was masked by a positive association with nest desertion leading to no net  
815 reproductive benefits (Cole et al. 2012). We observed high levels of nest failure due to either  
816 abandonment or natural death of offspring among birds that expressed dear enemy behaviour, which

817 may be an indication of such a cost, although the likelihood of nest failure was not significantly different  
818 from birds that did not express dear enemy behaviour. However, perhaps a more likely reason for no  
819 observed effect is that our fitness measures were for a single breeding season, but typically selection  
820 varies over time (Siepielski et al. 2009). Similarly, we examined the initial stages of formation of dear  
821 enemy relationships and it may be that variation in the strength and specificity of relationships with  
822 neighbours over the course of the whole breeding season is more consequential for fitness, although  
823 these temporal dynamics and their relationship with fitness have not been explored. Third, although our  
824 measures of dear enemy behaviour had a high (albeit non-significant) repeatability coefficient,  
825 suggesting the possibility of intrinsic differences among individuals, in reality our measure was likely to  
826 have been influenced by other factors—for example temporary environmental effects—making it more  
827 difficult to identify links between dear enemy behaviour and variation in fitness (Zsebók et al. 2017).  
828 And finally, alterations to the experimental design, such as using a taxidermic mount to simulate visual  
829 cues (Ritschard et al. 2012; Araya-Ajoy et al. 2016) or carrying out the playbacks for more than three  
830 days, may have revealed additional individual variation that is more directly linked to dear enemy  
831 behaviour.

832

833 Dear enemy behaviours are undoubtedly adaptive and may well be under current selection in many  
834 systems, especially in species such as the great tit where territorial behaviour is important (Krebs 1971;  
835 Falls et al. 1982; McGregor and Avery 1986; Grabowska-Zhang et al. 2012b). Despite the intrinsic  
836 differences among individuals in their tendency to reduce the response to a familiar stimulus and then  
837 respond to a novel stimulus, none of these behaviours showed any positive or negative association with  
838 a variety of life history traits. However, revealing hypothetical links on behavioural traits such as the  
839 dear enemy effect that are likely underpinned by a variety of mechanisms, including cognitive  
840 mechanisms that themselves influence other functional behaviours, is likely to be more challenging than

841 for behaviours more closely related to reproduction, and to require a multivariate and longer-term  
842 approach across different ecological conditions (Morand-Ferron et al. 2016).  
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848  
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850 playbacks, MSR, GLD, IGK, JMC and JON collected breeding data, ED, CS and KvO did the DNA extractions  
851 and analyses of paternity, MSR analyzed the data, and MSR wrote the manuscript with input from all  
852 authors. Note that middle authors on this manuscript are listed in alphabetical order by surname.

853  
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863  
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- 1171

1172 **Table S1.** Study site locations and summary statistics.

1173

Site Name	Coordinates	N DE behaviour/N tested	Clutch Size	N Fledged	Average Mass (g)
Ballinphellic (BP)	51.840546, -8.630297	0/1	6	5	16.8
Castle Bernard (CB)	51.741568, -8.767775	2/9	5.0 (1.3)	1.4 (1.8)	14.4 (3.1)
Dukes Wood (DW)	51.785965, -8.751366	2/9	4.4 (1.1)	1.7 (1.7)	16.6 (1.9)
Dunderrow (DD)	51.719555, -8.600512	0/4*	5	0	15.3
Garrettstown (GT)	51.655159, -8.616456	0/1	6	6	18.0
Innishannon (IN)	51.763415, -8.664943	2/9	5.9 (1.5)	1.0 (1.6)	15.4 (1.6)
Kilbrittain (KB)	51.671290, -8.682011	8/16**	4.9 (1.3)	2.2 (2.0)	15.9 (1.6)
Shippool (SP)	51.737780, -8.630792	1/2	4.5 (0.7)	0.5 (0.7)	17.6

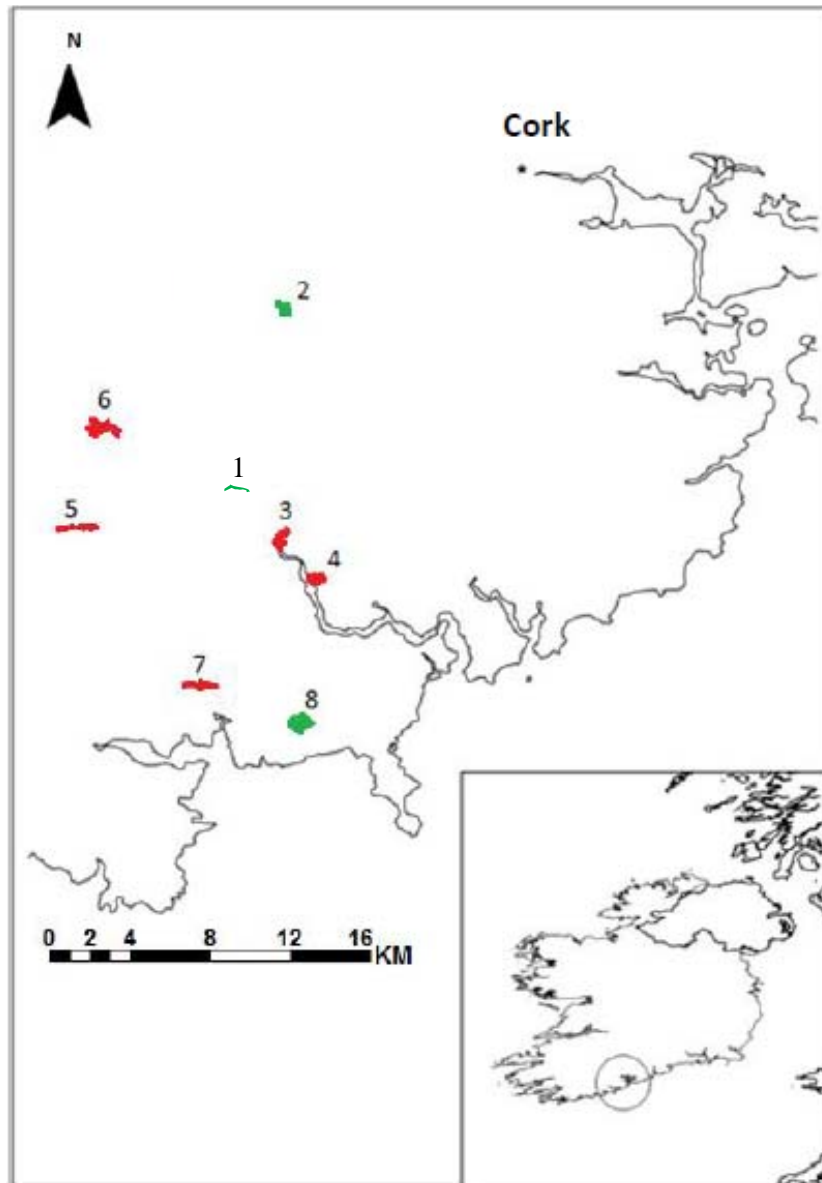
1174

1175 Site names and coordinates as in O'Shea 2017. See also Figure S1. Values for the reproductive success variables are means ( $\pm$ standard deviation,  
1176 not reported when only one individual was sampled at a site). Clutch size includes all eggs whether or not they were identified as extrapair;  
1177 number fledged and average mass were calculated excluding any young identified as extrapair. Initials for the site name are given that  
1178 correspond to the site variable in the raw data file. N DE behaviour refers to the number of individuals exhibiting dear enemy behaviour under  
1179 the standard criterion.

1180

1181 \*Three of these individuals at Dunderrow were excluded from the analyses of reproductive success variables because of widespread stoat  
1182 predation of nests at the site in 2018. The numbers reported here are from the one nest that was included.

1183 \*\*One individual from Kilbrittain that had no eggs in the nest was excluded from the calculations of reproductive success variables.



1184  
1185

1186 **Figure S1.** Map of the study sites, modified from O'Shea (2017). Numbers correspond to the individual  
1187 sites (see also Table S1): 1. Innishannon, 2. Ballinphellic, 3. Shippool, 4. Dunderrow, 5. Castle Bernard, 6.  
1188 Dukes Wood, 7. Kilbrittain, 8. Garrettstown.

1189 **Table S2.** Response on last neighbour trial versus response on stranger trial  
1190

	Responded stranger trial	Did not respond stranger trial
Responded last neighbour trial	15	0
Did not respond last neighbour trial	15	21

1191  
1192 The table shows the number of individuals for each combination of responding or not responding to the  
1193 last neighbour trial and to the subsequent stranger trial.

1194 **Table S3.** Effects of context on dear enemy behaviour.  
1195

Dear enemy criterion	Factor	Estimate	SE	Test statistic	P
Standard criterion	Intercept	1049	1668	0.63	0.53
	Year	-0.52	0.83	-0.63	0.53
	Date	0.07	0.05	1.33	0.18
	Stimulus rate (high)	0.58	0.70	0.82	0.41
	Date relative to first egg	-0.01	0.06	-0.18	0.86
	Average song number	-0.07	0.06	-1.13	0.26
Standard without nonresponders	Intercept	5701	3478	1.64	0.10
	Year	-2.83	1.73	-1.64	0.10
	Date	0.15	0.10	1.52	0.13
	Stimulus rate (high)	0.87	1.08	0.81	0.42
	Date relative to first egg	-0.02	0.08	-0.26	0.80
	Average song number	-0.25	0.12	-2.09	0.04
Response slope	Intercept	12.37	73.49	0.17	0.87
	Year	-0.01	0.04	-0.17	0.87
	Date	0.001	0.002	0.46	0.65
	Stimulus rate (high)	0.01	0.03	0.29	0.77
	Date relative to first egg	0.002	0.002	1.05	0.3
	Average song number	0.002	0.002	1.00	0.33
Song slope	Intercept	485	2262	0.21	0.83
	Year	-0.24	1.12	-0.22	0.83
	Date	0.08	0.07	1.13	0.27
	Stimulus rate (high)	-0.70	0.81	-0.86	0.40
	Date relative to first egg	0.01	0.06	0.12	0.91
	Average song number	0.05	0.05	0.96	0.35

1196  
1197 Results are from a generalized linear model of whether or not the individual met the standard criterion  
1198 for expressing dear enemy behaviour (where the test statistic is  $z$ ), or from linear models for the slope  
1199 variables (where the test statistic is  $t$ ). The reference category for stimulus rate is the low rate stimulus.  
1200 The variable “average song number” refers to the average number of songs produced by the bird over  
1201 the nine total neighbour trials. Date is coded as the day number of the year on which the first playback  
1202 was performed for that bird, with 1 March being day 1. Date relative to first egg refers to which day the  
1203 first playback was performed for that bird relative to when the first egg was laid in the nest (so day zero  
1204 would indicate that the first playback was performed on the same day that the first egg was laid in the  
1205 nest).  $N = 50$  individuals for the standard criterion (one individual not included because there was never  
1206 an egg laid at the nest), 29 individuals for standard without nonresponders, and 25 individuals for the  
1207 slope variables.

1208 **Table S4.** Full models of dear enemy behaviour and reproductive success, including brood size effects when included in models.  
 1209

Reproductive measure	Dear enemy behaviour measure	Estimate(SE)	test statistic	P	N
Clutch size	Standard criterion	-0.14 (0.15)	-0.98	0.33	47
	Standard without nonresponders	-0.15 (0.17)	-0.85	0.40	28
	Response slope	0.59 (1.29)	0.46	0.65	28
	Song slope	0.008 (0.043)	0.19	0.85	28
Number fledged	Standard criterion	-0.42 (0.35)	-1.22	0.22	47
	Standard without nonresponders	-0.33 (0.37)	-0.90	0.37	28
	Response slope	3.12 (2.13)	1.47	0.14	28
	Song slope	0.04 (0.07)	0.58	0.56	28
Fledged offspring yes/no	Standard criterion	-0.85 (0.65)	-1.30	0.19	47
	Standard without nonresponders	-0.58 (0.76)	-0.75	0.45	28
	Response slope	-1.48 (5.73)	-0.26	0.80	28
	Song slope	0.04 (0.19)	0.19	0.85	28
Average offspring biomass (g)	Standard criterion	-0.78 (0.94)	-0.83	0.41	30
	Brood size	0.28 (0.27)	1.06	0.30	
	Standard without nonresponders	0.69 (1.11)	0.62	0.55	16
	Brood size	0.46 (0.34)	1.35	0.2	
	Response slope	-7.00 (9.64)	-0.73	0.48	16
	Brood size	0.62 (0.46)	1.36	0.2	
	Song slope	0.09 (0.33)	0.27	0.79	16
	Brood size	0.28 (0.49)	0.58	0.57	
Individual offspring mass (g)	Standard criterion	-0.70 (0.92)	-0.76	0.45	95/30
	Brood size	0.20 (0.26)	0.75	0.46	
	Standard without nonresponders	0.77 (0.99)	0.78	0.45	49/16
	Brood size	0.38 (0.31)	1.24	0.24	
	Response slope	-7.00 (8.81)	-0.79	0.44	49/16
	Brood size	0.57 (0.44)	1.28	0.22	
	Song slope	0.01 (0.30)	0.05	0.96	49/16
	Brood size	0.29 (0.47)	0.62	0.55	

1210  
1211 Output is from models with the reproductive measure as the dependent variable (all measures except for clutch size include only within-pair  
1212 young), and the dear enemy behaviour measure as a factor. Models for average and individual offspring mass included brood size as an  
1213 additional factor (brood size never had a significant effect; results reported in Table S3). Test statistic is  $z$  for analyses of clutch size and number  
1214 fledged, and  $t$  for the remaining reproductive measures. Sample sizes refer to the number of subject males included (for the analyses of  
1215 individual offspring mass they refer to the number of individual offspring/number of subject males) and vary because some variables excluded  
1216 individuals that failed to respond to both the final neighbour playback and the stranger playback (“nonresponders”), and because for many nests  
1217 all offspring died before weighing on day 15. For the standard criteria, the reference category was individuals that did not show dear enemy  
1218 behaviour. Statistically significant effects are shown in bold.



1219 **Table S5.** Full models of dear enemy behaviour and reproductive success. Unlike Table S4, these analyses include both within-pair and extra-pair  
 1220 young.  
 1221

Reproductive measure	Dear enemy behaviour measure	Estimate(SE)	test statistic	P	N
Number fledged	Standard criterion	-0.45 (0.30)	-1.50	0.13	47
	Standard without nonresponders	-0.36 (0.33)	-1.08	0.28	28
	Response slope	2.75 (2.02)	1.36	0.17	28
	Song slope	0.06 (0.07)	0.80	0.42	28
Fledged offspring yes/no	Standard criterion	-0.69 (0.65)	-1.07	0.29	47
	Standard without nonresponders	-0.59 (0.77)	-0.76	0.45	28
	Response slope	-2.75 (5.84)	-0.47	0.64	28
	Song slope	0.04 (0.19)	0.23	0.82	28
Average offspring biomass (g)	Standard criterion	-0.77 (0.86)	-0.89	0.38	31
	Brood size	0.31 (0.26)	1.19	0.25	
	Standard without nonresponders	0.69 (1.00)	0.69	0.50	17
	Brood size	0.47 (0.31)	1.52	0.15	
	Response slope	-5.89 (8.62)	-0.68	0.51	17
	Brood size	0.57 (0.40)	1.45	0.17	
	Song slope	0.11 (0.29)	0.38	0.71	17
	Brood size	0.28 (0.41)	0.67	0.51	
Individual offspring mass (g)	Standard criterion	-0.70 (0.83)	-0.85	0.41	111/31
	Brood size	0.22 (0.25)	0.89	0.38	
	Standard without nonresponders	0.75 (0.91)	0.83	0.42	59/17
	Brood size	0.38 (0.29)	1.33	0.21	
	Response slope	-5.68 (7.99)	-0.71	0.49	59/17
	Brood size	0.48 (0.38)	1.26	0.23	
	Song slope	0.06 (0.26)	0.23	0.82	59/17
	Brood size	0.23 (0.38)	0.59	0.56	

1222  
 1223 Output is from models with the reproductive measure as the dependent variable (all measures include both extra-pair and within-pair young),  
 1224 and the dear enemy behaviour measure as a factor. Results for clutch size are not reported here because the identical analysis is already

1225 presented in Table S4 (we did not remove extra-pair young from the measure of clutch size). Models for average and individual offspring mass  
1226 included brood size as an additional factor (brood size never had a significant effect; results reported in Table S3). Test statistic is  $z$  for analyses  
1227 of clutch size and number fledged, and  $t$  for the remaining reproductive measures. Sample sizes refer to the number of subject males included  
1228 (for the analyses of individual offspring mass they refer to the number of individual offspring/number of subject males) and vary because some  
1229 variables excluded individuals that failed to respond to both the final neighbour playback and the stranger playback (“nonresponders”), and  
1230 because for many nests all offspring died before weighing on day 15. For the standard criteria, the reference category was individuals that did  
1231 not show dear enemy behaviour. Statistically significant effects are shown in bold.

1232 Supplementary References

1233

1234 O'Shea, W. 2017. The evolutionary ecology of personality and life history variation in an anthropogenic

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