1   No reproductive benefits of dear enemy recognition in a territorial songbird

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21   ABSTRACT

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23   Territorial animals often exhibit the dear enemy effect, in which individuals respond less aggressively to

24   neighbours than to other individuals. The dear enemy effect is hypothesized to be adaptive by reducing

25   unnecessary aggressive interactions with individuals that are not a threat to territory ownership. A key

26   prediction of this hypothesis, that individual fitness will be affected by variation in the speed and extent

27   to which individuals reduce their aggression towards neighbours relative to strangers, has never been

28   tested. We used a series of song playbacks to measure the change in response of male great tits on their

29   breeding territories to a simulated establishment of a neighbour on an adjacent territory. Males reduced

30   their approach to the speaker and sang fewer songs on later repetitions of the playback trials, consistent

31   with a dear enemy effect through habituation learning. However, not all males discriminated between

32   the neighbour and stranger playbacks at the end of the series of trials, and there was evidence that

33   individuals consistently differed from one another in performing this discrimination. We monitored

34   nests and analysed offspring paternity to determine male reproductive success. Unexpectedly,

35   individuals that exhibited dear enemy behaviour towards the simulated neighbour did not have higher

36   reproductive success, and in fact one measure, total offspring biomass, was lower for individuals that

37   showed the dear enemy effect. Although the general capability to recognize neighbours is most likely

38   adaptive, it seems that individuals who decrease their responsiveness to familiar neighbours too quickly

39   may gain no advantage or even be at a disadvantage.

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

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43   INTRODUCTION

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45   Territorial animals live in a social environment in which they may benefit by responding differently to

46   their territorial neighbours than they do to other individuals (McGregor, 1993). For instance, many

47   species show 'dear enemy effects', in which individuals respond less aggressively towards neighbours

48   than towards strangers (Stoddard, 1996; Temeles, 1994; Tumulty, 2018; Ydenberg et al., 1988). A

49   leading hypothesis for the evolution of the dear enemy effect is that it is adaptive because it enables

50   territory holders to avoid wasted time, energy and injury risk in aggressive interactions with individuals

51   that are not a threat because they hold their own territory (the 'threat level' hypothesis (Getty, 1987;

52   Temeles, 1994)). This hypothesis predicts that intraspecific variation in the speed and extent to which

53   individuals reduce their aggression towards non-threatening neighbours will affect individual fitness.

54   However, this key prediction has never been tested, and indeed the fitness consequences of neighbour

55   recognition have mostly been studied indirectly, for instance by demonstrating that individuals holding

56   territories with long-term neighbours have higher reproductive success than those with new neighbours

57   (Beletsky & Orians, 1989; Grabowska-Zhang, Sheldon, et al., 2012; Grabowska-Zhang, Wilkin, et al.,

58   2012; Siracusa et al., 2021). The dear enemy effect is far from ubiquitous among species. In some

59   species, individuals respond more aggressively to neighbours than strangers (Bruintjes et al., 2016;

60   Muller & Manser, 2007; Temeles, 1990), and in others they do not discriminate between them at all

61   (Battiston et al., 2015; Bee, 2003a; Tumulty et al., 2018). Within species, variation in the expression of

62   the dear enemy effect is often context dependent (Courvoisier et al., 2014; Hyman, 2005; Pratt &

63   McLain, 2006), but these studies examined population-level responses, and individual variation and its

64   fitness consequences have not been measured. Thus, while it is clear that neighbour recognition

65   systems vary and have evolved, there is still a limited understanding of the selection pressures that have

66   driven this evolution, especially at the within-species level.

67

68   The dear enemy effect is facilitated by mechanisms for neighbour recognition learning (Wiley, 2013).

69   Thus, variation among individuals in the expression of the dear enemy effect (i.e. the extent and speed

70   with which aggression is reduced towards neighbours relative to strangers) may arise because of

71   variation in cognitive abilities associated with neighbour recognition. If this cognitive variation affects

72   reproductive success, for instance if those individuals on breeding territories that quickly learn to

73   recognize their neighbours can invest the time and energy saved by avoiding unnecessary agonistic

74   encounters into their offspring, then individuals with superior cognitive ability for neighbour recognition

75   will have higher fitness and be favoured by selection. However, non-cognitive factors also affect the

76   expression of the dear enemy effect. For instance, individuals may differ in aggressiveness or other

77   personality traits, and context-dependent factors such as territory size and the density of neighbouring

78   territory-holders also likely affect responsiveness to neighbours (Amy et al., 2010; Jacobs et al., 2014;

79   Pratt & McLain, 2006; Yoon et al., 2012). Regardless of the source, this individual variation in dear

80   enemy expression has potentially significant, but unexplored, consequences for fitness. Furthermore,

81   few studies have examined the trajectory over which the dear enemy effect develops upon

82   establishment of a new neighbour (Bee & Gerhardt, 2001a), but this time period in which relationships

83   are being established is likely when individual differences will be greatest, and have strongest effects on

84   fitness.

85

86   Like many songbirds, great tits (*Parus major*) defend territories around their nest during the breeding

87   season (Gosler, 1993). Male great tits defend territories by singing and approaching intruding individuals

88   to engage in visual displays and occasionally, physical fighting (Blurton Jones, 1968; Krebs, 1977). Great

89   tits nest in natural cavities or artificial nest boxes, and the primary threat from intruders is the potential

90   for them to usurp the limited resource of a high-quality nesting location (Krebs, 1971, 1976, 1982),

91   although intruders also present other threats including potentially mating with the territory-holder's

92   social mate (Hill et al., 2011) or foraging on the territory (Hinde, 1956). The dear enemy effect has been

93   demonstrated previously in great tits: in playback experiments, individuals showed a reduced response

94   to songs of their territorial neighbours compared to songs of strangers (Falls et al., 1982; Krebs, 1971;

95   McGregor & Avery, 1986), and the effect was stronger when the neighbour's song was played from its

96   actual territory (McGregor & Avery, 1986). Recognition of neighbours in great tits is not based on a

97   simple discrimination between the categories of familiar and unfamiliar individuals (Wiley, 2013);

98   instead they can learn to discriminate among the songs of different specific individuals (McGregor &

99   Avery, 1986; Weary & Krebs, 1992). There is also among-individual variation in aggressive responses to

100   playback resulting from personality differences (Amy et al., 2010). Great tits trade off the time invested

101   in foraging and territory defence (Ydenberg, 1984; Ydenberg & Krebs, 1987); thus, individuals that

102   rapidly reduce their aggression towards their neighbours may benefit directly by increasing their

103   foraging intake, and this in turn could enhance their ability to provision for their offspring (Martin,

104   1987). However, vigilance must be maintained against potential territorial usurpers, because the longer

105   a usurper is on the territory, the more effort is required to expel it (Krebs, 1982).

106

107   To determine whether individual variation in dear enemy behaviour affects reproductive success, we

108   performed a series of acoustic playback experiments in which we monitored territorial males' responses

109   to the simulated arrival of a new male on a neighbouring territory. We broadcast the playback stimulus

110   multiple times across three days to determine if males' responses to the playback declined over time,

111   and tested whether any decline was specific to the song used as the playback stimulus and therefore

112   consistent with discrimination between neighbours and strangers under the dear enemy effect. We

113   classified individuals as either expressing dear enemy behaviour or not after nine repetitions of the

114   playback, and then monitored each male's nest to test the prediction that individuals that rapidly

115   reduced their response to neighbours would have higher reproductive success in terms of number of

116   offspring fledged and/or nestling mass, which is positively correlated with subsequent survival

117   (Tinbergen & Boerlijst, 1990). We also examined the paternity of nestlings to determine if the reduction

118   in aggressive response towards neighbours affected males' abilities to defend against extrapair

119   copulations. By using experiments in a wild population to test a key prediction for the adaptive function

120   of the dear enemy effect, we provide novel insights into a widespread territorial defence behaviour.

121

122   METHODS

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124   Playbacks were performed during the spring breeding season (April-May in 2017 and 2018) in eight

125   small forestry plots in County Cork, Ireland (Table S1). Each site contained an array of nestboxes, which

126   are preferentially used by great tits for breeding (East & Perrins, 1988). We identified potential playback

127   subjects by listening for males singing near nestboxes, and examining the progress of nest building in the

128   box. Males chosen for the experiment were then subject to a series of song playbacks as described

129   below.

130

131   The project received ethical approval from the Animal Welfare Body at University College Cork (HPRA

132   license number AE19130-P017), and was in accordance with the ASAB (Association for the Study of

133   Animal Behaviour) Guidelines for the Treatment of Animals in Behavioural Research and Teaching. All

134   research was conducted under licenses from the National Parks and Wildlife Service of Ireland and the

135   British Trust for Ornithology as part of ongoing research in these populations.

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137   *Playback procedure*

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139   Male great tits sing on territories containing their nesting site. Males typically have a repertoire of

140   approximately three to four distinctive song types (Gompertz, 1961; McGregor & Krebs, 1982b).

141   However, during a song bout they usually repeat the same song type for several minutes before

142   switching to a different song type (Krebs, 1976). The playbacks were designed to mimic this repetition of

143   a single song type. Although simulating a larger song repertoire through playbacks may have captured

144   additional aspects of the dear enemy phenomenon, this was not necessary to address our primary aims

145   and would have reduced our power to detect dear enemy behaviour because: 1. Males habituate to the

146   presentation of both a single song type and multiple song types, but habituation is slower to playback of

147   multiple song types (Krebs, 1976), and 2. Males will respond to the presentation of a single song type in

148   a manner consistent with the dear enemy effect: responding more strongly to a single song type of a

149   stranger than to a single song type of an established neighbour (Krebs, 1971).

150

151   The playback stimuli consisted of recordings of natural male songs made using Wildlife Acoustics SM4

152   audio recorders (24 kHz sampling rate) placed at nestboxes in May 2016. We scanned audio files for

153   exemplars of male songs with a high signal to noise ratio and containing no other bird songs in the

154   background. We inserted each chosen song into a new audio file in Audacity software, bandpass filtered

155   the song between 1.5 and 11.5 kHz, and manipulated the song to contain 6 phrases (the basic repeating

156   unit of the song (McGregor & Krebs, 1982a)) by copying or deleting phrases as needed. The song

157   exemplar was then copied so that it was played back at a rate of either five ("low rate treatment") or ten

158   ("high rate treatment") songs per minute for five minutes. These two stimulus rates were used to test

159   the prediction that the likelihood of recognition learning depended on the stimulus repetition rate

160   (Thompson & Spencer, 1966). A total of 29 song exemplars were chosen, and each exemplar was

161   recorded at a different nestbox; songs came from seven of the eight study sites. The playback stimulus

162   selected for the subject male and the song rate treatment were chosen randomly, with the restriction

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163   that the stimulus song was not recorded from the same site as the subject (all sites were at least 2.25

164   km apart from each other; Table S1). This ensured that subjects would not have been familiar with the

165   playback song already. Stimuli were broadcast as .wav files from an EasyAcc X02s speaker mounted on a

166   tripod at approximately 1 m height, at a sound-pressure level of 90 dB (A) measured at 1 m using an

167   Extech 407730 sound level meter.

168

169   On each of three consecutive days we exposed males to three playbacks, performed at 1 hour intervals,

170   of one of the playback stimuli (Figure 1). Each subject was therefore exposed to a total of nine playbacks

171   of the same stimulus (henceforth the "neighbour" stimulus), which simulated a newly arrived male on a

172   neighbouring territory. Playbacks were performed between 0800h and 1540h; each male was tested at

173   approximately the same time on each of the three days of the experiment. The playbacks were always

174   performed from the same location, and at a distance of 25 m from the nestbox. This location was

175   chosen because territoriality is likely strongest near the nestbox (Giraldeau & Ydenberg, 1987), 50 m is a

176   typical nearest-neighbour distance (Krebs, 1971), and neighbour-stranger discrimination is typically

177   strongest near the territorial border (Falls & Brooks, 1975; Stoddard et al., 1991). We therefore

178   standardized the absolute distance of the speaker from the territory's centre in order to standardize

179   sound amplitude at the nestbox for all males. There is an inevitable trade-off between the advantages of

180   this approach and those of estimating males' actual territorial boundaries and placing the speaker at

181   each male's estimated territorial edge. Both for logistical reasons and because absolute stimulus

182   intensity is likely to play a role in the speed of dear enemy learning (Bee, 2001), we used a standardized

183   playback distance. The specific location of the playback was chosen in a randomized direction, with the

184   constraint that playbacks were only performed from areas the experimenter could access, and that did

185   not overlap with the territory of another male great tit.

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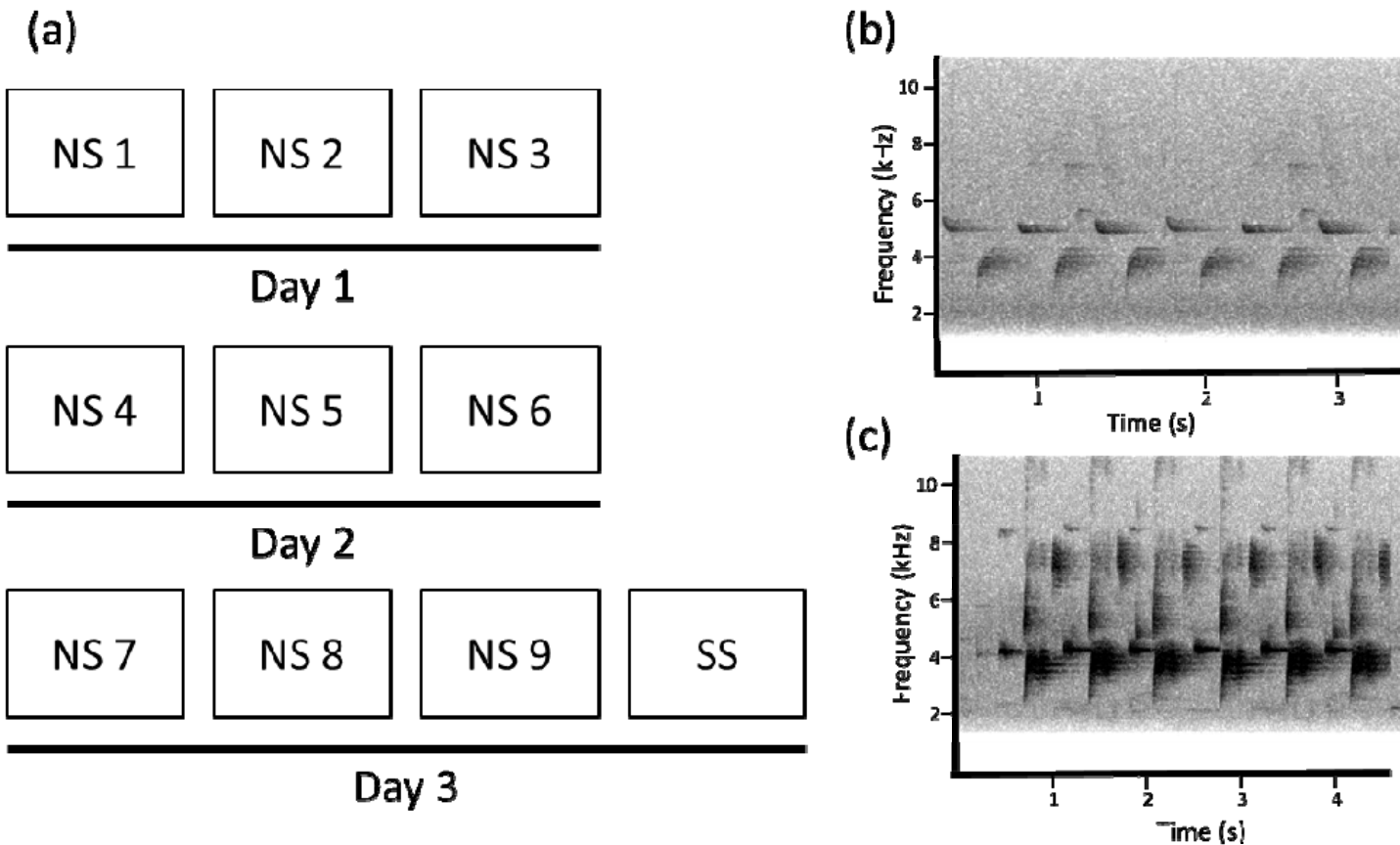
Figure 1. (a) Timeline of the playback experimental design. We broadcast the neighbour stimulus ('NS') for five minutes per trial (number in each

box corresponds to the trial number), for a total of three trials per day with approximately one hour between trials. This procedure was

repeated for three consecutive days. On the third day, immediately following the final neighbour playback (NS 9), we broadcast a different song

from a different location ('SS': stranger stimulus, a test of stimulus specificity). In 2017, the entire procedure was repeated with different stimuli

192   after a period of ten days to test the repeatability of dear enemy behaviour. (b) Exemplar playback stimulus. The spectrogram shows a single

193   great tit song that was used to build one of the playback stimuli. (c) a second exemplar stimulus, taken from a different bird, illustrating the

194   acoustic variation in great tit songs that allows for dear enemy recognition. An example playback experiment could use the song in (b) for the

195   neighbour stimulus and that in (c) for the stranger stimulus. Note that the spectrograms do not illustrate the equalization of playback amplitude

196   that was used for the trials.

197   During each playback we monitored males' behaviour and made audio recordings of any songs using

198   Marantz PMD 660 or PMD 661 audio recorders with Sennheiser ME67 directional microphones (16 bit,

199   44.1 kHz sampling rate). We noted the closest approach of the male to the playback speaker, in

200   categories of 5 m (Nelson & Soha, 2004). Subjects were not always located at the nestbox at the start of

201   the playback, so approach distances greater than 25 m were possible. Individuals that did not respond at

202   all were given a value of "None" for approach distance, which in the ordinal analyses described below

203   was considered the greatest distance. From the audio recordings we counted the number of songs

204   produced by the male during the playback. We considered males to have responded to the playback if

205   they sang at any point during the stimulus broadcast, or made any movement towards the playback

206   speaker, and to have not responded if they did neither of those. The final dataset included 51

207   individuals; data from the first trial recording for one bird included in this total were lost because of a

208   faulty microphone cable.

209

210   On the third day, immediately after the ninth exposure of the subject to the neighbour stimulus, we

211   broadcast a different song stimulus from a different location (still 25 m away from the nestbox). The aim

212   was to compare the response to this new stimulus, simulating a new stranger individual (henceforth, the

213   "stranger" stimulus), to the original playback stimulus to which we hypothesized the subject would have

214   developed some familiarity towards. This is an essential step for demonstrating individual recognition in

215   territorial systems, in which individuals reduce their response to familiar neighbours, but maintain a

216   heightened response to an unfamiliar stranger (Bee et al., 2016).

217

218   In 2017 only, we repeated this three-day procedure with 20 individuals ten days after their final trial

219   from the first round of playbacks. The aim of this repetition was to investigate whether the expression

220   of dear enemy behaviour was repeatable. Therefore, we performed playbacks as above, but with a

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221   different song stimulus from a different location, simulating a different new neighbour establishing a

222   territory. A different stranger stimulus was also used in these repeated trials, and the male was given

223   the opposite rate treatment of what it had been exposed to during the first round of playbacks.

224

225   *Criterion for dear enemy recognition*

226

227   The classical method for demonstrating the dear enemy effect is to, in a single trial, present individuals

228   with the signals of an actual established neighbour, followed by a single trial presentation of the signals

229   of an individual that the subject would not have interacted with (Battiston et al., 2015; Brunton et al.,

230   2008; Wei et al., 2011). The dear enemy effect is inferred when individuals have a reduced response to

231   the neighbour stimulus compared to the stranger stimulus. In our protocol we simulated the

232   establishment of a new neighbour through a series of playbacks, which essentially served as training

233   sessions to give the subject the opportunity to learn to recognize its neighbour. Therefore, to test

234   whether or not the subject was indeed exhibiting dear enemy behaviour at the end of the necessarily

235   fixed number of trials, we used the classical criterion for testing the dear enemy effect: comparison of

236   the response to a final neighbour playback and a stranger playback. Our criterion (hereafter referred to

237   as the 'standard criterion') that the subject was expressing dear enemy behaviour was that it did not

238   respond in the final (ninth) playback of the simulated neighbour, but then did respond to the

239   subsequent playback of a simulated stranger.

240

241   Although we argue that our criterion effectively identifies individuals that recognized their neighbour

242   and were expressing dear enemy behaviour towards it, we recognize that this binary criterion has

243   limitations as a metric of dear enemy expression. Therefore, we explored additional measures of an

244   individual's change in response towards its neighbour over time. First, in some cases individuals

245   responded to neither the final neighbour playback nor the stranger playback. These results are difficult

246   to interpret because it may indicate a general loss of motivation to defend the territory rather than a

247   failure to discriminate neighbours and strangers. We therefore repeated all analyses, defining dear

248   enemy behaviour as above, but only including those birds that responded to the stranger stimulus

249   (referred to as the 'standard criterion without nonresponders'; no individual failed to respond to the

250   stranger playback after responding to the final neighbour playback). Second, for each individual, we

251   extracted slope parameters from a logistic regression of the binary response variable on trial number

252   (not including the stranger playback), and a linear regression of the number of songs on trial number.

253   The aim was to obtain a more quantitative estimate of the change in response across trials that may

254   reveal more variation than our binary criterion. If individuals have developed dear enemy recognition of

255   the newly-established neighbour, these values would be expected to be negative, indicating a decline in

256   response across trials. However, a decline in response to a neighbour is not sufficient to demonstrate

257   the dear enemy effect, because individuals must continue to respond to strangers. Therefore, we only

258   included individuals that responded to the stranger playback for these analyses.

259

260   *Breeding data*

261   Breeding data were obtained as part of standard monitoring protocols for the project (O'Shea et al.,

262   2018). We recorded the date when the first egg was laid, the total clutch size, date of hatching and

263   number of fledglings. The identity of the subject male sometimes could be determined by identification

264   of unique colour rings, if the male had already been captured prior to the experiment. Some males were

265   also identified by the use of RFID-equipped nestbox entrance doors, which could read the unique

266   passive integrated transponder tag placed on the leg of previously captured males. Males could also be

267   identified when breeding adults were caught at the nest for ringing and measurements, 10-12 days after

268   the eggs hatched. Fifteen subjects were not identified because the male was not tagged, the nest was

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269   abandoned prior to trapping, or the male could not be caught. However, our analyses do not rely on

270   knowing the specific identity of the subject, and we can safely assume that no male was recorded in the

271   study more than once based on the timing and distribution of boxes at which playbacks were carried out

272   across the eight sites. Breeding densities are low at our sites and in cases where males could not be

273   identified by color rings we nevertheless consider it highly unlikely that more than one individual

274   responded to the playback on different trials. Chicks were weighed at day 15, and we determined the

275   number of fledglings by inspecting the nest for any dead chicks after the breeding attempt was

276   complete.

277

278   *Paternity analysis*

279

280   Estimates of reproductive fitness in birds depend on levels of extra-pair paternity (EPP) (Webster et al.,

281   1995). Although rates of EPP are relatively low in great tits (Patrick et al., 2012; van Oers et al., 2008),

282   they could have altered the relationship between dear enemy behaviour and reproductive success,

283   particularly as paternity loss is one of the potential costs of territorial intrusions, and neighbours and

284   strangers may differ in the threat they pose to paternity (Schlicht et al., 2015). EPP levels may also

285   influence selection on males to cooperate via dear enemy effects (Eliassen & Jørgensen, 2014). We

286   therefore analyzed males' reproductive success using metrics that excluded any offspring that were

287   identified in a paternity analysis as being extra-pair offspring.

288

289   DNA was obtained from feathers taken from breeding pairs and offspring on their respective dates of

290   capture and ringing. DNA extraction was performed using the protocol of the E.Z.N.A. Tissue DNA Kit

291   (Omega Bio-Tek, Norcross, GA, USA), with the exception of the use of 80 µL elution buffer on a single

292   elution step. Samples were genotyped at eight microsatellite loci, selected based on previously observed

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293   variability and utility, as well as potential for multiplexing in a single reaction (Pma69u (k=7 alleles)

294   (Kawano, 2003); PmaD22 (k=20), PmaCan1 (k=15), PmaGAn30 (k=5), PmaC25 (k=19), PmaTAGAn86

295   (k=19), PmaTGAn33 (k=17) and PmaTGAn45 (k=11) (Saladin et al., 2003)). Multiplex PCR was performed

296   in a 3.5 µl total volume, including 1 µl of DNA extract, and 1.75 µl of 2x Top-Bio™ Plain Combi PP

297   Mastermix, with a concentration of 0.03 µM for the Pma69U, PmaCan1, PmaGAn30 and PmaTAGAn86

298   primers and 0.06 µM for the PmaC25, PmaD22, PmaTGAn33 and PmaTGAn45 primers. The PCR was

299   programmed with an initial denaturation at 95°C (15 min) followed by five cycles of 94°C (30 s), 55°C (90

300   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

301   60°C for 30 min. The PCR products were diluted in 14 µL nuclease free water; and run on an Applied

302   Biosystems ABI3500xl DNA analyser using POP-7 polymer with GeneScan™ 600 LIZ™ Dye Size Standard

303   v2.0 (ThermoFisher Scientific). We used GeneMarker version 2.7.0 software (SoftGenetics, Pennsylvania,

304   USA) to determine allele sizes.

305

306   Paternity was assigned using CERVUS version 3.0.7 software (Kalinowski et al., 2007) using 10,000 cycles,

307   94 candidate fathers, a 0.02% error rate, two candidate parents and 93% of loci typed as simulation

308   parameters. Only individuals that were successfully genotyped at five or more loci were included in

309   paternity analyses. Individuals were determined to be within-pair offspring if all loci matched those of

310   the social father and social mother combination, or if there was a mismatch at only one of the loci but

311   the social father was identified as the most likely father using critical trio LOD scores returned by the

312   program. Offspring that did not meet these criteria were categorized as extra-pair offspring. We

313   assumed that offspring whose paternity was not determined (9 of 96 fledged offspring and 13 of 111

314   weighed offspring were of unknown paternity; two offspring fledged but were not weighed or analysed

315   for paternity because they fledged on the day of weighing) were within-pair offspring. The combined

316   exclusion probability for all eight microsatellites was >99.99%. Two of our loci significantly deviated from

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317   Hardy-Weinberg equilibrium when the genotypes of all individuals in the analysis were included

318   (PmaC25: χ^2 = 40.98, df = 15, p < 0.001, PmaD22: χ^2 = 33.87, df = 15, p = 0.004). This was likely due to

319   the family structure of the data.

320

321   *Data analysis*

322   Except for the analyses of repeatability (see below), all analyses were performed only on the first

323   repetition of the playback trials (i.e., we excluded data from the repetition of the procedure that was

324   performed in 2017 only). We address the following questions in our analyses:

325

326   1. Does the response to the neighbour playback decrease over time? We tested whether males reduced

327   their aggressiveness as they became more exposed to the songs of other males using three different

328   variables, all of which have been demonstrated to be related to the aggressive response in great tits in

329   previous studies (Amy et al., 2010; Doutrelant et al., 2000; McGregor & Avery, 1986; Snijders et al.,

330   2016): "response", i.e. whether the male responded at all by singing or approaching (binary), approach

331   distance (ordinal categorical), and number of songs during individual trials. In all cases the trial number

332   (1-9) and stimulus rate treatment (low or high) were entered as a fixed effects and individual identity as

333   a random effect. Response was modelled using a binomial generalized linear mixed model using the

334   glmer function in the lme4 version 1.1-23 package (Bates et al., 2015) in R 4.0.2 software (R

335   Development Core Team, 2021). Approach category was modelled using a cumulative link mixed model

336   to account for the ordinal nature of the dependent variable using the clmm function in the ordinal

337   2019.12-10 package (Christensen, 2019). Number of songs was modelled as a poisson variable using the

338   glmmTMB function of the glmmTMB 1.0.2.1 package (Brooks et al., 2017), which accounts for zero

339   inflation in the dataset.

340

341   2. Is there a difference in the response to the stranger playback compared to the final (ninth) familiar

342   neighbour playback? If there was a decrement in aggression in the analyses above, the next step to

343   demonstrate the dear enemy effect is to show that this decrement is stimulus specific. Therefore,

344   individuals were predicted to respond more strongly to the stranger playback than to the final

345   neighbour playback. We tested the same variables as above, using the same analyses but with the trial

346   variable a factor with two levels: final neighbour or stranger playback trial.

347

348   3. Is there a difference in reproductive success between individuals that did or did not express dear

349   enemy behaviour? We ran separate models for each of five different metrics of reproductive success,

350   and each of the four measures of dear enemy behaviour (see *Criterion for dear enemy recognition*,

351   above). For these analyses, we excluded data from three males from one of the sites (Dunderrow, see

352   Table S1) in 2018 because of widespread nest predation. Although predation is certainly a component of

353   reproductive success, in this site almost every nest was completely predated by stoats, and therefore we

354   consider that there could be no relationship between the male phenotypic characteristics under study

355   and the survival of offspring in this site with unusually high predation, rendering reproductive measures

356   of these individuals meaningless in the context of our hypotheses.

357

358   In all reproductive success models we included whether or not the individual exhibited dear enemy

359   behaviour, as defined above, as a fixed factor. Initial models also included the date the first egg was laid

360   in the clutch, with the first of March as day 1, as well as the date of the first playback trial relative to the

361   first egg date, but neither of these variables ever explained variation in reproductive success and so

362   were excluded from the final models (the lack of an effect of first egg date was unexpected, but see

363   (O'Shea et al., 2018) for an explanation). 1. Clutch size was modelled as a poisson variable in a

364   generalized linear model. For one subject, no eggs were laid at the nestbox, and it was given a clutch

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365   size value of zero, as well as zeroes for the other measures of reproductive success described next. 2.

366   Number of within-pair fledglings was a poisson variable, but there were a large number of zero values.

367   We therefore modelled it accounting for zero-inflation as above. 3. The sum total of the mass of all

368   within-pair offspring in the nest on day 15. There were a large number of zero values because in many

369   nests all chicks died, in which case the nest was assigned a total biomass of zero, so this continuous

370   variable was modelled with a tobit regression using the censReg function in the censReg 0.5-30 package

371   (Henningsen, 2019). One nest was removed from this analysis because two offspring were observed

372   fledging on the day of weighing, and therefore were not weighed, so an accurate measure for this

373   variable could not be obtained 4. Average mass of within-pair offspring on day 15. Although this

374   measure may be more straightforward than the total mass analysis described above, it has the

375   disadvantage of excluding the large number of subjects (N=18) whose nests failed entirely before day

376   15. This reduces sample size and also excludes individuals facing the most severe fitness consequences.

377   We entered average offspring mass as the dependent variable in a linear model with an additional factor

378   of brood size (including both within- and extra-pair offspring). 5. The actual mass of each individual

379   within-pair offspring. This analysis also excludes failed nests, but may reveal important variation in

380   parental investment among those nests that did survive. Individual mass was entered as a Gaussian

381   variable in a linear mixed model, with brood size as an additional factor.

382

383   Initial models with site included as a random effect could not be run because of singularity issues,

384   because there were few samples from most sites (see Table S1). For the same reason, we did not

385   perform a formal analysis of reproductive success by site, but there were no obvious qualitative

386   differences in these variables between the four sites with the largest numbers of individuals tested

387   (Table S1).

388

18

389   We estimated the repeatability of dear enemy recognition behaviour using the rptR package (Nakagawa

390   & Schielzeth, 2010) with the repetition (first or second) and stimulus rate treatment as fixed factors,

391   individual as a random factor and whether the individual did or did not exhibit the dear enemy effect

392   (standard criterion) as a binary dependent variable. One individual was removed from this analysis

393   because it did not respond during any trial in the second repetition. Repeatabilities of the response and

394   song slope measures were analysed similarly, but with the dependent variable modelled as Gaussian.

395   Finally, we used a binomial generalized linear model to test whether there were differences between

396   individuals that did or did not exhibit the dear enemy effect (standard criterion) in the proportion of

397   fledglings that were extra-pair.

398

399 RESULTS

400

401 *Change in response to the neighbour playback*

402 The likelihood of a response (either or both of singing or moving towards the speaker) significantly

403 decreased across the neighbour playback trials (Table 1; Figure 2A). The pattern of responses shows an

404 initial slight increase in the likelihood of responding over the first few trials, and then larger decreases

405 especially in the final trials of the day. Approach distance was significantly greater on later trials, such

406 that individuals were more likely to make a close approach to the speaker on earlier trials, and

407 approached but stayed further away or did not approach at all on later trials (Table 1). Likewise, the

408 number of songs produced by males during the playback decreased across trials (Table 1; Figure 2B).

409 There was no effect of stimulus rate on response or approach distance, but there was a non-significant

410 trend for an effect on the number of songs, with males giving more songs in response to stimuli

411 presented at the higher rate (Table 1).

412

413

414   Table 1. Tests of change in response to neighbour playback across trials.

415

Variable	Factor	Estimate (SE)	z	P
Response	Intercept	0.53 (0.27)		
	Trial number	−0.10 (0.04)	−2.52	0.01
	Rate	0.04 (0.28)	0.13	0.89
Approach distance	Trial number	0.11 (0.04)	3.10	0.002
	Rate	−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	0.23 (0.12)	1.89	0.058

416

417

418   Output is from a generalized linear mixed model for Response (binary), a cumulative link mixed model

419   for approach distance (distances were placed into ordinal categories), and a zero-inflated glmm for

420   number of songs (Poisson; the coefficients are for the conditional model output). The reference

421   category for stimulus rate is the low rate, so positive estimates indicate more responses and a greater

422   number of songs, and a greater distance from the speaker, in response to the high rate stimulus. Trial

423   number was entered as a numerical variable. N = 51 individuals.
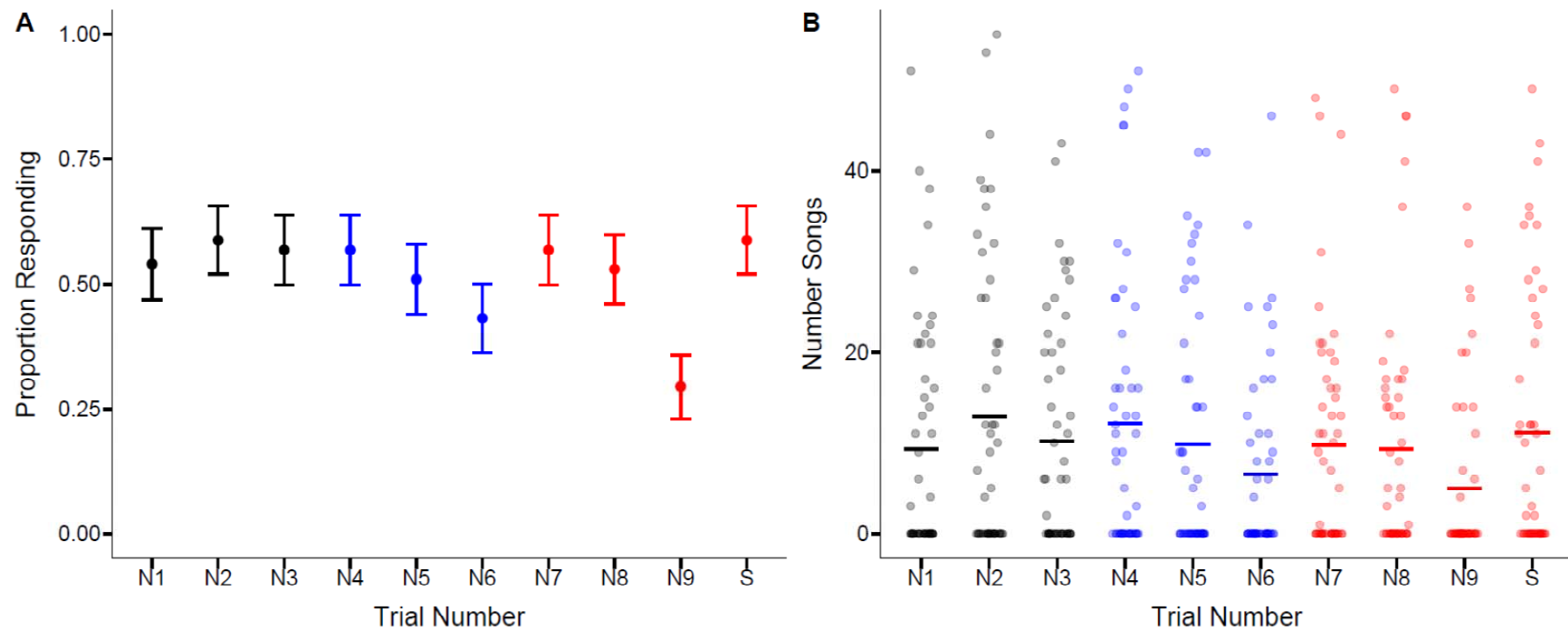
Figure 2. Response across trials. (A) The proportion (±SE) of individuals (*N* = 51 for all trials except *N* = 50 for N1; see Methods) that responded by either singing or approaching the playback speaker in each of the nine neighbour playback trials (labelled N1-N9) and on the stranger playback trial. Colours correspond to the day that the playback was performed (black = day 1, blue = day 2, red = day 3). (B) The number of songs produced by males during the playback trial. Dots represent an individual's response to that trial (points have been jittered along the x-axis and rendered partially transparent for ease of interpretation). Horizontal lines represent mean values.

431   *Stimulus specificity of response to neighbour playback*

432

433   Although twice as many individuals responded to the stranger playback compared to the immediately

434   preceding final neighbour playback, this difference was not significant (Figure 2A; Table 2). However,

435   there was a significant difference in both the approach distance and number of songs between the final

436   neighbour playback and the stranger playback: individuals approached closer and sang more songs in

437   response to the stranger playback (Figure 2B; Table 2). Stimulus rate did not affect the responses when

438   only these two trials were considered (Table 2).

439

440

441

442   Table 2. Tests of stimulus specificity of response to neighbour playback.

443

Variable	Factor	Estimate (SE)	z	P
Response	Intercept	−2.54 (2.51)		
	Trial	3.59 (3.33)	1.08	0.28
	Rate	−0.12 (1.42)	−0.08	0.94
Approach distance	Trial	−2.09 (0.56)	−3.73	<0.001
	Rate	0.13 (0.79)	0.17	0.87
Number of songs	Intercept	−0.04 (0.74)		
	Trial	0.30 (0.08)	3.56	<0.001
	Rate	0.04 (0.92)	0.04	0.97

444

445   Output is from models as in Table 1, but now only including the response to the final neighbour playback

446   and the stranger playback. Trial was therefore coded as a binary variable. The reference category for

447   trial is the final neighbour playback, so positive estimates would indicate more responses and a greater

448   number of songs, and a negative estimate indicates closer approach, during the stranger playback. The

449   reference category for stimulus rate is the low rate. $N = 51$ individuals.

450

451

452

453   *Dear enemy behaviour and reproductive success*

454

455   Based on our standard criterion of no response to the final neighbour playback followed by a response

456   to the stranger playback, 15 of 51 individuals exhibited dear enemy behaviour towards their simulated

457   neighbour after the nine playbacks (15 of 30 when non-responders were removed i.e. standard criterion

458   without nonresponders, see Methods; these results refer only to the first set of playbacks, and do not

459   include the second set of playbacks that were performed in 2017). Whether an individual met the

460   standard criterion did not depend on the date of testing, the date relative to the day on which the first

461   egg was laid, the year or the stimulus rate (Table S2). These variables also did not affect the slope of the

462   response or number of songs across trials (Table S2). There was also no effect of age (first year versus

463   older) on meeting the standard criterion for dear enemy behaviour (Estimate of effect being older than

464   first year ± SE = −1.29 ± 0.88, z = −1.46, P = 0.15; N = 33 individuals of known age). However, there was

465   an effect of age on the slope of number of songs across trials, with older birds having a more positive

466   slope than first year birds (Estimate = 2.96 ± 0.83, t = 3.57, P = 0.003; N = 17 individuals of known age),

467   and also on the slope of responses across trials (Estimate = 0.07 ± 0.03, t = 2.33, P = 0.03; N = 17). There

468   was a trend for significant repeatability in whether an individual exhibited dear enemy behaviour, with a

469   moderate repeatability coefficient (*N* = 19 individuals tested twice; R = 0.44, P = 0.074). Five of six

470   individuals that showed dear enemy behaviour in the first set of playbacks also did so in the second, and

471   six of 13 individuals that did not show dear enemy behaviour in the first set of playbacks also did not

472   show it in the second set. There were insufficient numbers of individuals tested twice and responding to

473   the stranger playback to allow for estimating the repeatability of the slope for response or number of

474   songs across trials.

475

476   Sixteen offspring were identified as extra-pair young and were excluded from the analyses of number of

477   offspring fledged and offspring mass. There was no difference between individuals that did or did not

478   show dear enemy behaviour in the proportion of fledglings that were extrapair (Estimate = 0.20 ± 0.71,

479    $P = 0.78$, $N = 29$ nests). There was no effect of whether an individual exhibited dear enemy behaviour

480   (standard criterion) on the number of eggs laid in its nest (Figure 3A; Table S3), or on the number of

481   within-pair offspring that fledged (Figure 3B; Table S3). However, the total mass of all within-pair

482   offspring weighed at day 15 was significantly lower for individuals that showed dear enemy behaviour

483   towards the simulated neighbour (Figure 3C; Estimate = −38.2 ± 15.4, P = 0.01, $N = 47$ nests). For the

484   limited set of individuals that fledged young, there was no effect of whether it had met the standard

485   criterion for dear enemy behaviour on the average mass of its within-pair offspring (Figure 3D; Table S3)

486   or on the individual mass of within-pair offspring (Table S3). Qualitatively similar results were obtained

487   when the standard criterion without nonresponders was used as the response variable (Table S3). When

488   the slope of responses or number of songs across trial was used as the response variable, there were no

489   significant effects on any of the reproductive success measures (Table S3).
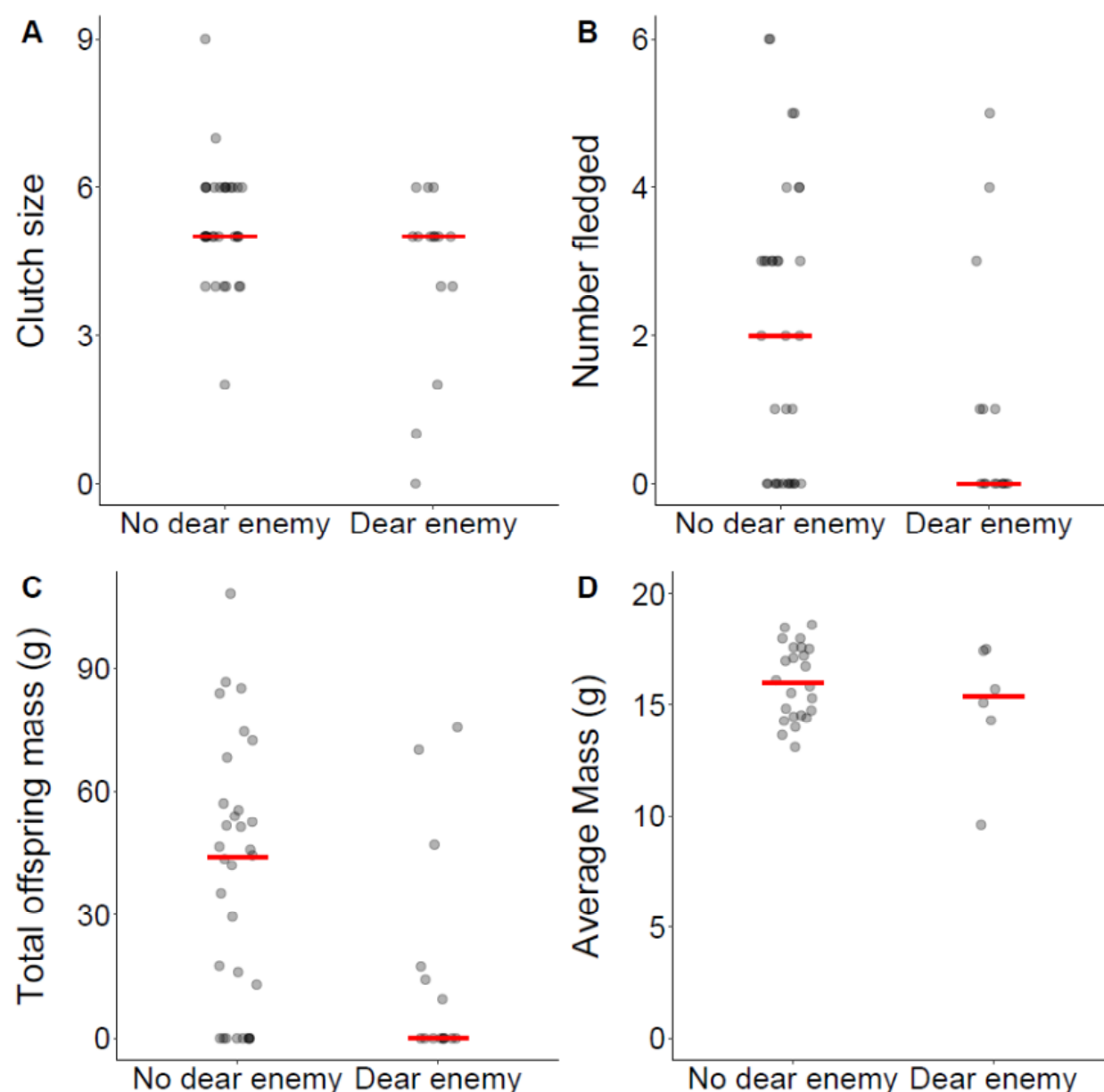
490

491 Figure 3: Relationship between whether the individual met the standard criterion (see Methods) for

492 exhibiting the dear enemy effect ("Dear enemy") or not ("No dear enemy") and different measures of

493 reproductive success. Each dot represents the value for an individual nest (points jittered along the x-

494 axis and rendered partially transparent); red horizontal line represents the median. A. Clutch size, B.

495 Number of within-pair offspring successfully fledged, C. Total mass of within-pair offspring at day 15

496 post hatch, D. Average mass of within-pair offspring at day 15 post hatch (not including nests for which

497   no offspring survived to day 15). N = 48 individuals in each graph, except for C where N = 47 and D

498   where N = 30.

499

500   DISCUSSION

501

502   Male great tits in our study populations exhibited behaviour consistent with the dear enemy effect in

503   response to playbacks of a simulated territorial neighbour. There was an overall decline in song

504   response and approach towards the playback across repeated presentations, consistent with reduced

505   aggression towards an increasingly familiar individual. This reduced aggression was stimulus-specific

506   because in the stranger playback, simulating a different individual, subjects reverted to a strong

507   response to the playback. Our experiments show that individual recognition can arise and be expressed

508   in only three days. However, not all birds exhibited dear enemy behaviour towards the simulated

509   neighbour at the end of the playback trials. This individual variation in response to neighbours had an

510   unexpected association with reproductive output: there was no reproductive benefit for individuals that

511   exhibited dear enemy behaviour in any case. Furthermore, there may in fact have been a reproductive

512   cost paid by these individuals: birds that showed the dear enemy effect had significantly reduced total

513   fledgling biomass and the number of offspring fledged was also lower, if not significantly so. Below we

514   discuss these results in the context of territorial aggression and the evolution of neighbour recognition.

515

516   *Learning mechanisms and individual variation*

517

518   The dear enemy effect is widespread in animals (Dimarco et al., 2010; Fox & Baird, 1992; Jaeger, 1981),

519   although most studies demonstrate the effect by comparing responses to one-time playbacks of songs

520   of actual neighbours versus strangers (Lambrechts & Dhondt, 1995). Playback experiments simulating a

521   new neighbour and monitoring in detail the change in subjects' responses across trials are a potentially

522   powerful, but rarely utilized, tool to study the mechanism of neighbour recognition. There is a cognitive

523   component to the dear enemy effect in great tits, and while we recognize that non-cognitive

524   mechanisms may also contribute to variation in whether an individual responds differently to

525   neighbours and strangers (see below), it is worthwhile to discuss the cognitive mechanism of dear

526   enemy recognition in light of our experimental design and results.

527

528   Habituation learning has been demonstrated to mediate dear enemy recognition in many species. For

529   instance, in an extensive series of experiments, playbacks were used to show that the dear enemy effect

530   in bullfrogs (*Rana catesbeiana*) is mediated by habituation learning of specific characteristics of

531   neighbour vocalizations (Bee, 2001, 2003b; Bee & Gerhardt, 2001b, 2001c, 2001a, 2002), and some

532   studies of songbirds have also supported a role of habituation in neighbour recognition (Brooks & Falls,

533   1975a; Petrinovich & Peeke, 1973). The pattern of response change across trials in our study matches

534   many of the characteristics of habituation (Rankin et al., 2009; Thompson & Spencer, 1966) and suggests

535   that habituation learning is the mechanism behind the initial stages of dear enemy recognition in great

536   tits. First, the response to repeated playback of a simulated neighbour decreased across trials (Figure 2).

537   Second, there was evidence for spontaneous recovery of the response across days, in which the

538   response on the first trial of the day was generally greater than that of the last trial on the previous day

539   (Figure 2). A key characteristic of habituation is that over a series of recoveries and decrements,

540   habituation is potentiated, with the response decrement becoming ever more pronounced (Rankin et

541   al., 2009; Thompson & Spencer, 1966). Although we had only nine testing sessions across three days,

542   comparisons of behaviour on day 2 and day 3 show that the response decrease was much greater on

543   day 3, consistent with a potentiation of habituation effect. Third, the dual-process theory of habituation

544   argues that in addition to the decrement in response caused by habituation, an independent process of

29

545   sensitization results in an initial, but transient, increase in aggressive response (Groves & Thompson,

546   1970; Petrinovich & Patterson, 1982). Consistent with sensitization, responses tended to be weaker on

547   the first playback trial compared to the subsequent few trials.

548

549   One possible exception for a role of habituation in explaining our results is that habituation is

550   hypothesized to develop faster at higher stimulus repetition rates (Groves & Thompson, 1970;

551   Thompson et al., 1973), but although males in the high rate treatment sang more overall, there was no

552   effect on approach or whether individuals exhibited dear enemy recognition at the end of the playback

553   trials. However, while we varied the rate of repetition of songs within a trial, the interval between

554   successive trials was approximately the same for all birds. Finally, while we argue that our findings are in

555   many ways consistent with a habituation mechanism, as are those in other species (Bee & Gerhardt,

556   2001a; Brooks & Falls, 1975b), this may only apply to the initial stages of neighbour recognition. That

557   neighbour songs can be remembered and discriminated across years (McGregor & Avery, 1986), and

558   that individuals are capable of learning to recognize individual voice characteristics and discriminate

559   among even previously unheard songs (Weary & Krebs, 1992), along with the finding that individuals

560   with strong social associations formed during winter flocking tend to end up on neighbouring breeding

561   territories (Firth & Sheldon, 2016), suggests that other cognitive abilities such as associative learning are

562   also important in long-term neighbour recognition in great tits (see also (Godard, 1991; Richards, 1979)).

563

564   Whatever the mechanism, our results indicate that at an individual level, only some of the males

565   reduced their aggression towards the simulated neighbour and discriminated between it and a

566   simulated stranger. If this variation was due to differences in recognition learning ability, then additional

567   trials per day, or less time in between trials perhaps could have facilitated learning for a greater

568   proportion of the population (Petrinovich & Patterson, 1982), although this approach would have

569   constrained our ability to test a sufficient number of individuals in the field. Moreover, the simultaneous

570   presentation of a visual stimulus (e.g., taxidermy mount of great tit male), playbacks with interactive

571   elements (Langemann et al., 2000), or playbacks presenting the full song repertoire of a simulated

572   neighbour rather than a single song type (Krebs, 1976; Weary & Krebs, 1992), may provide more intense

573   stimulation, thus facilitating more pronounced learning effects as well as exposing additional individual

574   variation in responses (Araya-Ajoy et al., 2016; Ritschard et al., 2012).

575

576   However, there are also many plausible non-cognitive explanations for variation in whether males

577   showed the dear enemy effect. Differences in overall aggressiveness are likely to be particularly

578   important; even if individuals learned to recognize their neighbour, they may maintain an overall more

579   aggressive response. Such variation in aggressiveness is known to affect response to playback in great

580   tits (Araya-Ajoy & Dingemanse, 2014). Males also likely differ in previous experience and this could have

581   affected their response to playback simulating a new neighbour in several ways. For instance, although

582   we assigned playback stimuli randomly and only exposed individuals to songs from different

583   populations, some males may have happened to have been given a playback stimulus more similar

584   acoustically to songs of a previous neighbour, affecting whether they reduced their response over time.

585   Males likely varied in the extent to which they had already interacted with different territorial

586   neighbours in the past, and great tits with more previous exposure to songs of many neighbours are

587   slower to learn to recognize new neighbours (McGregor & Avery, 1986). We do not have data on the

588   songs of individuals' previous neighbours to test these possibilities directly, although we note that there

589   was no difference in dear enemy effect expression between first-year birds and older birds in our study.

590   Other context-based plasticity (e.g. density, progress of the breeding season) can explain variation in the

591   dear enemy effect (Hyman, 2005; Pratt & McLain, 2006; Yoon et al., 2012), and has been reported in one

592   study of great tits (Jin et al., 2020). However, we found no effect of year, date or date relative to the

593   start of hatching on whether individuals expressed the dear enemy effect. Furthermore, we found some

594   evidence of individual repeatability in the expression of the dear enemy effect despite our small sample

595   size, which suggests that despite context-dependent variation there is some consistent among-individual

596   variation in neighbour recognition behaviour in this species.

597

598   *Dear enemy recognition and fitness*

599

600   We hypothesized that if the dear enemy effect is adaptive because it reduces time spent in unnecessary

601   aggressive interactions (Getty, 1987; Temeles, 1994), then individuals that reduce the aggression

602   directed towards their neighbours more quickly would have higher reproductive success. This

603   hypothesis was not supported: we found either no effect at all, or an effect in the opposite direction

604   than predicted. Specifically, individuals that expressed the dear enemy effect had lower total chick

605   biomass, but there was no difference in clutch size, average biomass, or number of offspring that

606   fledged. Mass of the chicks is related to parental foraging effort (Schwagmeyer & Mock, 2008) and is an

607   important component of fitness because heavier chicks are more likely to survive after fledging

608   (Tinbergen & Boerlijst, 1990).

609

610   It is not clear why individuals that did not show dear enemy recognition had higher total offspring

611   biomass. It may be that these individuals were of overall higher quality, and could therefore afford to

612   put more effort into territorial defence while still foraging effectively, which may have resulted in larger

613   and more exclusive territories for subsequent offspring provisioning. Even if there were no quality

614   differences among individuals, if there is variation in territory quality, then individuals on higher quality

615   territories potentially had more to lose (Riechert, 1984), and therefore maintained an aggressive

616   response for longer to ensure they could hold on to the territory. In this case, the expression of the dear

617   enemy effect is only indirectly related with offspring quality, because the relationship is mediated by

618   joint correlations between both variables and territory quality. One caveat is that our fitness measures

619   only cover a single breeding season. Because of trade-offs between current and future reproduction

620   (Trivers, 1972), fitness effects of dear enemy expression may be more apparent over the lifetime

621   reproductive output and this should be addressed in future studies.

622

623   There may be costs associated with rapid reductions in aggressive responses that counteract any

624   benefits of reduced aggression towards neighbours. In particular, individuals that are too quick to

625   reduce their aggression may be ineffective at driving off prospecting individuals, perhaps resulting in

626   compromised territory size and quality. In our experiment, individuals that displayed the dear enemy

627   effect did so after exposure to only one song type and only three days of singing by the simulated newly-

628   arrived neighbour, potentially taking the risk of reducing aggression without fully assessing the

629   individual via its entire song repertoire and over a longer time period (Getty, 1989). It may therefore be

630   beneficial to maintain heightened aggression until territorial boundaries are well established. Individuals

631   that quickly reduce aggression may also be more susceptible to their mates engaging in extrapair

632   copulations with neighbours; we found no such relationship, although a greater sample size may be

633   necessary to detect any effect. Alternatively, the association between poor offspring quality and rapid

634   expression of the dear enemy effect may reflect high costs of the cognitive abilities associated with

635   neighbour recognition learning (Morand-Ferron et al., 2016). Birds that expressed the dear enemy effect

636   very often had failed nests (Figure 3B), although the difference in number of offspring fledged between

637   birds that did and did not show dear enemy behaviour was not significant. Nest failure is generally high

638   in our populations (O'Shea et al., 2018) and although we accounted for the zero values statistically, the

639   results suggest that some of the difference in our measures of reproductive success may be due to a

640   greater susceptibility to nest abandonment in birds showing the dear enemy effect (Figure 3B). Similar

33

641   differences in the likelihood of abandonment have been demonstrated in the context of variation in

642   innovative problem solving behaviour in great tits (Cole et al., 2012).

643

644   The lack of a reproductive benefit (and potential cost, as indicated by the results for total offspring

645   biomass) for birds showing the dear enemy effect in this study should not necessarily be taken as

646   evidence that selection does not favour the ability to discriminate neighbours from strangers. Dear

647   enemy recognition is well-established in great tits (Falls et al., 1982; Krebs, 1971; McGregor & Avery,

648   1986), and individuals with a higher proportion of familiar neighbours (i.e., those they had already been

649   a neighbour of in a previous year) had higher reproductive success (Grabowska-Zhang, Wilkin, et al.,

650   2012). Although many birds did not express dear enemy behaviour within the timeframe of the

651   experiment, we expect that with additional exposures, most individuals would have expressed a robust

652   dear enemy effect, as they do towards playbacks of long-established natural neighbours (Krebs, 1971). If

653   individuals that were already showing the dear enemy effect within the short timeframe of the

654   experiment did suffer reduced reproductive success, as some of our results suggest, then we argue that

655   selection may be acting on the rate at which individuals reduce the response to neighbours, favouring

656   males that more gradually reduce their aggressive response. This may or may not involve variation in

657   recognition learning capabilities: as described above, some individuals may have remained aggressive

658   despite having learned to recognize their neighbour.

659

660   *Conclusions*

661

662   The dear enemy effect is the outcome of dynamic interactions between neighbouring individuals. While

663   progress has been made in understanding between-species differences in responses to territorial

664   neighbours (Bee et al., 2016; Christensen & Radford, 2018; Tumulty & Bee, 2020), the understanding of

34

665   the causes and consequences of within-species variation in dear enemy behaviour has lagged behind.

666   Our finding of either no relationship, or in some cases a negative relationship, between dear enemy

667   recognition and reproductive success, along with the moderate repeatability of the expression of the

668   dear enemy effect, indicates that there could be fitness costs to reducing aggression towards neighbours

669   too quickly. Although challenging, additional work along the lines of our study that monitor the

670   development of dear enemy relationships between neighbours and associate this with individual

671   phenotypic characteristics and reproductive success will be essential for understanding a widespread

672   and consequential form of social behaviour in animals.

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687

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945

946   Table S1. Study site locations and summary statistics.

Site Name	Coordinates	N DE behaviour/N tested	Clutch Size	N Fledged	Total Mass (g)	Average Mass (g)
Ballinphellic (BP)	51.840546, −8.630297	0/1	6	5	83.8	16.8
Castle Bernard (CB)	51.741568, −8.767775	2/9	5.0 (1.3)	1.4 (1.8)	33.5 (38.7)	14.4 (3.1)
Dukes Wood (DW)	51.785965, −8.751366	2/9	4.4 (1.1)	1.7 (1.7)	29.3 (28.0)	16.6 (1.9)
Dunderrow (DD)	51.719555, −8.600512	0/4*	5	0	45.9	15.3
Garrettstown (GT)	51.655159, −8.616456	0/1	6	6	108.0	18.0
Innishannon (IN)	51.763415, −8.664943	2/9	5.9 (1.5)	1.0 (1.6)	19.2 (20.8)	15.4 (1.6)
Kilbrittain (KB)	51.671290, −8.682011	8/16	4.6 (2.1)	2.1 (2.0)	33.6 (31.4)	15.9 (1.6)
Shippool (SP)	51.737780, −8.630792	1/2	4.5 (0.7)	0.5 (0.7)	8.8 (12.4)	17.6

947   Site names and coordinates as in O'Shea (2017). Values for the reproductive success variables are means (±standard deviation, not reported

948   when only one individual was sampled at a site). Clutch size includes all eggs whether or not they were identified as extrapair; number fledged,

949   total mass and average mass were calculated excluding any young identified as extrapair. Failed nests in which no offspring survived to day 15

950   (aside from the three excluded from Dunderrow, see below) were given a value of 0 for total mass, but were not included in calculations of

951   average mass. Initials for the site name are given that correspond to the site variable in the raw data file. N DE behaviour refers to the number of

952   individuals exhibiting dear enemy behaviour under the standard criterion.

953   *Three of these individuals at Dunderrow were excluded from the analyses of reproductive success variables because of widespread stoat

954   predation of nests at the site in 2018. The numbers reported here are from the one nest that was included.

955

956   Table S2. Effects of context on dear enemy behaviour.

957

Dear enemy criterion	Factor	Estimate (SE)	Test statistic	P
Standard criterion	Year	−0.73 (0.81)	−0.91	0.37
	Date	0.08 (0.05)	1.50	0.13
	Stimulus rate (high)	−0.45 (0.67)	−0.66	0.51
	Date relative to first egg	−0.002 (0.06)	−0.03	0.98
Standard without nonresponders	Year	−2.47 (1.32)	−1.87	0.062
	Date	0.15 (0.07)	1.95	0.051
	Stimulus rate (high)	0.32 (0.85)	0.38	0.70
	Date relative to first egg	0.001 (0.068)	0.02	0.98
Response slope	Year	−0.003 (0.036)	−0.08	0.94
	Date	0.001 (0.002)	0.25	0.81
	Stimulus rate (high)	0.008 (0.026)	0.32	0.75
	Date relative to first egg	0.002 (0.002)	0.97	0.34
Song slope	Year	−0.14 (1.12)	−0.13	0.90
	Date	0.06 (0.07)	0.95	0.35
	Stimulus rate (high)	−0.68 (0.81)	−0.84	0.41
	Date relative to first egg	0.003 (0.06)	0.04	0.97

958

959   Results are from a generalized linear model of whether or not the individual met the standard criterion

960   for expressing dear enemy behaviour (where the test statistic is z), or from linear models for the slope

961   variables (where the test statistic is t). The reference category for stimulus rate is the low rate stimulus.

962   N = 50 individuals for the standard criterion (one individual not included because there was never an egg

49

963   laid at the nest), 29 individuals for standard without nonresponders, and 25 individuals for the slope

964   variables.

965   Table S3. Full models of dear enemy behaviour and reproductive success, including brood size effects when included in models.

966

Reproductive measure	Dear enemy behaviour measure	Estimate(SE)	test statistic	P	N
Clutch size	Standard criterion	−0.21 (0.15)	−1.45	0.15	48
	Standard without nonresponders	−0.21 (0.17)	−1.26	0.21	29
	Response slope	1.06 (1.29)	0.83	0.41	29
	Song slope	0.009 (0.043)	0.20	0.84	29
Number fledged	Standard criterion	−0.45 (0.35)	−1.27	0.21	48
	Standard without nonresponders	−0.35 (0.38)	−0.93	0.35	29
	Response slope	3.19 (2.14)	1.49	0.14	29
	Song slope	0.04 (0.07)	0.58	0.56	29
Total biomass (g)	Standard criterion	−38.2 (15.4)	−2.49	**0.01**	47
	Standard without nonresponders	−35.5 (18.2)	−1.95	0.051	29
	Response slope	139.0 (135.3)	1.03	0.30	29
	Song slope	3.84 (4.57)	0.69	0.49	29
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	30
	Brood size	0.20 (0.26)	0.75	0.46	
	Standard without nonresponders	0.77 (0.99)	0.78	0.45	16
	Brood size	0.38 (0.31)	1.24	0.24	
	Response slope	−7.00 (8.81)	−0.79	0.44	16
	Brood size	0.57 (0.44)	1.28	0.22	
	Song slope	0.01 (0.30)	0.05	0.96	16
	Brood size	0.29 (0.47)	0.62	0.55	

967

968   Output is from models with the reproductive measure as the dependent variable (all measures include only within-pair young), and the dear

969   enemy behaviour measure as a factor. Models for average and individual offspring mass included brood size as an additional factor (brood size

970   never had a significant effect; results reported in Table S3). Test statistic is z for analyses of clutch size and number fledged, and t for the

971   remaining reproductive measures. Sample sizes refer to the number of subject males included and vary because some variables excluded

972   individuals that failed to respond to both the final neighbour playback and the stranger playback ("nonresponders"), and because for many nests

973   all offspring died before weighing on day 15. For the standard criteria, the reference category was individuals that did not show dear enemy

974   behaviour. Statistically significant effects are shown in bold.

975   Supplementary References

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

978   heterogeneous landscape. PhD Thesis, University College Cork.

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