Cooperative nest building in wild jackdaw pairs

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Abstract

Animals create diverse structures, both individually and cooperatively, using materials from their environment. One striking example are the nests birds build for reproduction, which protect the offspring from external stressors such as predators and temperature, promoting reproductive success. To construct a nest successfully, birds need to make various decisions, for example regarding the nest material and their time budgets. To date, research has focused mainly on species where one sex is primarily responsible for building the nest. In contrast, the cooperative strategies of monogamous species in which both sexes contribute to nest building are poorly understood. Here we investigated the role of both sexes in nest building and fitness correlates of behaviour in wild, monogamous jackdaw pairs (*Corvus monedula*). We show that both partners contributed to nest building and behaved similarly, with females and males present in the nest box for a comparable duration and transporting material to the nest equally often. However, while females spent more time constructing the nest, males tended to invest more time in vigilance, potentially as a means of coping with competition for nest cavities. These findings suggest a moderate degree of division of labour, which may facilitate cooperation. Moreover, some aspects of behaviour were related to proxies of reproductive success (lay date and egg volume). Females that contributed relatively more to bringing material laid earlier clutches and pairs that spent less time together in the nest box had larger eggs. Thus, selection pressures may act on how nest building pairs spend their time and cooperatively divide the labour. We conclude that cooperative nest building in birds could be associated with monogamy and obligate biparental care, and provides a vital but relatively untapped context through which to study the evolution of cooperation.

Keywords

animal architecture; bird nest; construction behaviour; cooperation; *Corvus monedula*; division of labour; jackdaw; monogamy

Highlights

- In wild monogamous jackdaws, mates behaved similarly and cooperated to build their nest.
- Females built more and called more frequently; males tended to be more vigilant.
- Females that contributed relatively more to transporting nest material laid earlier clutches.
- Pairs that spent more time together in the nest box had smaller eggs.
- Cooperation may be crucial in light of obligate biparental care and nest site competition.

1. Introduction

Across the animal kingdom, species build structures for various purposes relevant for fitness. Such animal architecture (Hansell, 2005, 2007) is used in diverse contexts such as creating a protective shelter (Rosell et al., 2005), reproduction and parental care (Deeming & Reynolds, 2015), capture of prey (Hunt, 1996), and communication and signalling (Borgia, 1995). A striking example are bird nests built for reproduction (Collias, 1964; Collias & Collias, 1984; Hansell, 2000; Healy, Walsh, & Hansell, 2008), which influence fitness by protecting the offspring, for example from predators through camouflage (Bailey et al., 2015) and from environmental stressors, such as temperature (Collias, 1964). Additionally, nests can function as an intraspecific signal of investment in reproduction (Massoni et al., 2012; Soler et al., 1998) and to attract mates (Metz et al., 2009). While nest building behaviour was traditionally assumed to be genetically predetermined (Nickell, 1958), recent evidence highlights an important role for learning (Bailey et al., 2014; Breen et al., 2016; Walsh et al., 2013). For example, male zebra finches (*Taeniopygia guttata*) adjust their preferred material based on their success in a past breeding attempt (Muth & Healy, 2011). However, research to date has focussed on species in which single individuals (often males) predominantly build

51 the nest: in zebra finches, for instance, studies have focused on males, who are responsible for bringing
52 the nest material (Zann, 1996). While both partners may then contribute to arranging the material in the
53 nest, their cooperative interactions at this stage have not been investigated in detail. While there has been
54 some work describing contributions to nest building in cooperative breeders like sociable weavers
55 (*Philetairus socius*) and white-browed sparrow-weavers (*Plocepasser mahali*) (Collias & Collias, 2008; Collias
56 & Collias, 1978) cooperative nest building by monogamous mates remains largely unexplored. This is
57 particularly surprising given that monogamy and biparental care are common in the majority of bird
58 species (Black, 1996; Reichard & Boesch, 2013). There is therefore a need to investigate whether and
59 how monogamous birds cooperate during nest building. This will allow us to comprehensively
60 understand the costs and benefits of cooperation between partners during this key stage of the breeding
61 cycle, and, more broadly, will allow a deeper insight into the cooperative behaviours underlying animal
62 architecture.

63 Effective cooperation between mates can be vital for fitness, particularly in species with obligate
64 biparental care (Griffith, 2019). However, the interests of both sexes do not align exactly, generating
65 sexual conflict (Chapman et al., 2003; Harrison et al., 2009). Research has concentrated largely on how
66 conflicts between mates are resolved when provisioning food to offspring (Hinde & Kilner, 2007; Iserbyt
67 et al., 2015; Johnstone et al., 2014), making monogamous birds central study systems to understand the
68 evolution of cooperative strategies. For instance, theoretical and empirical studies suggest that forms of
69 conditional cooperation, such as turn-taking, may serve to reduce conflicts of interest and stabilise
70 cooperation (Johnstone & Savage, 2019; Savage et al., 2017). Given that monogamous birds have long
71 served as important model systems for understanding the evolution of cooperation, and that mates in
72 some species are known to build the nest together (Birkhead, 2010; Massoni et al., 2012), it is striking
73 that cooperative nest building strategies have rarely been examined explicitly. Establishing the role of the
74 two sexes during cooperative nest building is crucial to our understanding of both cooperative strategies
75 and animal architecture.

76 In birds, the degree of cooperation between the sexes during nest building could be linked to the mating
77 system. For instance, in various polygynous weaver species (Ploceidae) males build nests alone to attract
78 females (Bailey et al., 2016), whereas in monogamous weavers mated pairs build their nest cooperatively
79 (Habig, 2020). Furthermore, two largely genetically monogamous species, Eurasian magpies (*Pica pica*)
80 (Parrot, 1995) and rufous horneros (*Furnarius rufus*) (Diniz et al., 2019), also build their nest cooperatively
81 (Birkhead, 2010; Massoni et al., 2012). However, fine-scale behaviours and time budgets have not
82 previously been explored, so cooperative nest building and its fitness consequences remain poorly
83 understood. The degree to which partners cooperate is likely to depend on how much their interests
84 align. In species showing obligate biparental care, mates should invest (relatively equally) in the offspring,
85 because a lack of investment by either parent is likely to lead to failure of the reproductive attempt
86 (Clutton-Brock, 2019). Moreover, one could expect greater degrees of cooperation in species with low
87 rates of extra-pair fertilisation (Lv et al., 2019), and high paternity certainty (Disciullo et al., 2019) as these
88 conditions create highly interdependent fitness outcomes. The success of a clutch could be impacted by
89 how bird pairs cooperate during nest building because cooperation may influence nest quality and because
90 this process is energetically and temporally costly and (Collias, 1964; Mainwaring & Hartley, 2013). The
91 energetic costs of nest building could vary between sexes due to differences in morphology, physiology,
92 energetic demands, and available information. Consequently, while both mates may behave similarly, sex-
93 based differences in the costs associated with certain activities could promote task specialisation, as
94 shown by evolutionary individual-based simulations of individuals providing two types of parental care
95 associated with a sex-based asymmetry regarding the costs (Barta et al., 2014). This could be important
96 in the context of nest building as well; for example, male magpies and female rufous horneros bring
97 relatively more material to the nest than the opposite sex. Investigating the roles of sexes, the level of
98 cooperation, whether cooperation is repeatable within pairs, and the fitness consequences during nest
99 building is also vital to further understand how individuals cope with the informational demands of
100 decision-making processes whilst tracking another individual's behaviour (Emery et al., 2007). Tracking
101 each other's behaviour could favour greater levels of behavioural synchrony, which could also be related

102 to behavioural compatibility between partners, potentially resulting in more effective cooperation and
103 greater reproductive success (Spoon et al., 2006).

104 Jackdaws (*Corvus monedula*) provide a particularly suitable study system to investigate cooperation during
105 nest building. They are a highly social, colony-breeding corvid that forms long-term pair bonds (Lorenz,
106 1931; Wechsler, 1989). Pairs produce one clutch per year, with both sexes providing care to altricial chicks
107 (Henderson & Hart, 1993). Moreover, unlike most socially monogamous bird species, jackdaws are
108 genetically monogamous, so the reproductive success of partners is more interdependent than in species
109 where extra-pair offspring occur (Gill et al., 2020). For jackdaws to reproduce successfully, they must
110 build a nest before egg laying commences. Jackdaws build nests within cavities, and these consist of a
111 platform (made of sticks) and a cup with soft material. Tightly linked fitness outcomes may generate
112 selection pressure for cooperation between partners throughout the breeding season, including during
113 the nest building stage.

114 This study had two main objectives: **(i)** To quantify behaviours and time budgets of pairs. We
115 hypothesised that birds should cooperate and share the workload to build the nest, because both
116 individuals should benefit from dividing costs and from a high-quality nest. Firstly, we predicted females
117 and males should behave similarly by investing in the nest directly (e.g. by bringing nest material) and
118 indirectly (e.g. through vigilance) (prediction 1). Secondly, however, we predicted that the time invested
119 in these behaviours may not be symmetrical between the sexes given morphological, physiological, and
120 informational differences (prediction 2). **(ii)** To examine the ultimate function of behaviours during nest
121 building by investigating three different fitness proxies: relative lay date, clutch size, and egg volume.
122 Laying earlier clutches can be advantageous and is often linked to reproductive success in birds (Perrins,
123 1965, 1970; Goumas et al., in prep.), for example because earlier layers face less competition in finding
124 food for their young. Larger eggs could potentially provide the embryo with more resources, aiding its
125 development and increasing the probability to survive (Krist, 2011). We hypothesised that how much
126 birds invest in their nest and how they share the workload could be associated with reproductive success,
127 with pairs that invest more overall and divide the labour (so that males contribute at least equally) being

128 favoured. While females should invest substantially in the nest because they may be better informed about
129 their requirements for incubation, males should contribute equally because this may allow females to
130 invest more resources in the clutch, potentially maximising reproductive success. Furthermore,
131 investment may determine the time to build the nest as well as its quality, which in turn could enhance
132 embryo development and survival. Firstly, we predicted that how pairs allocate their time between
133 different activities could impact fitness. More specifically, pairs investing more in the nest relative to other
134 activities, such as vigilance, should lay earlier, and have larger clutches and eggs (prediction 3). Moreover,
135 pairs that show greater total investment in the nest should lay earlier clutches (prediction 4). Pairs in
136 which males invest at least equally in the nest as well as in nest site defence should lay earlier and produce
137 larger clutches and eggs (prediction 5). If the optimal solution was for both individuals to invest equally,
138 one might expect a quadratic relationship between relative contributions of females compared to the
139 overall investment and fitness proxies. Finally, we predicted that jackdaws behaving more synchronously
140 by spending more time together in the nest box should lay earlier and have larger clutches and eggs
141 (prediction 6). As selection on nest building behaviours may depend on the degree to which they
142 constitute repeatable traits, we also investigated the repeatability of behaviour over time.

143

144 ## 2. Methods

145 ### Ethics Statement

146 This study was conducted with approval from the University of Exeter Biosciences Research Ethics
147 Committee (eCORN002970), following the ASAB Guidelines for the Treatment of Animals in
148 Behavioural Research (ASAB, 2012). Jackdaws had previously been colour ringed for individual
149 identification by qualified ringers licenced by the British Trust for Ornithology. The sex of each individual
150 was confirmed through molecular sexing of blood samples (Griffiths, Double, Orr, & Dawson, 1998)
151 under a UK Home Office licence (project licence 30/3261). Morphometrics of individuals, such as wing
152 length, tarsus length, and body weight, were measured when temporarily capturing birds for ringing (see

153 Greggor et al., 2017 for details). We used the exact age if birds were ringed as nestlings or juveniles, and
154 for adults that were already present when field sites were established in 2012, we assigned the maximum
155 age of eight years.

156 ## Data collection

157 As cavity nesters, jackdaws accept nest boxes and typically return to the same nest site across years,
158 allowing researchers to monitor behaviour by fitting boxes with video cameras. We recorded nest building
159 behaviour of free-living jackdaws using CCTV cameras with integrated microphones hidden inside nest
160 boxes during the breeding seasons of 2018 and 2019 at three breeding colonies in Cornwall, UK: X
161 (50°10'23"N; 5°7'12"W), Y (50°11'26"N, 5°10'51"W), and Z (50°11'56"N, 5°10'9"W). Nest boxes were
162 filmed slightly but significantly closer to the lay date in 2019 (mean ± SD = 7.69 ± 5.36 days) than in
163 2018 (10.83 ± 6.41 days) (LM, $\beta \pm SE = -3.136 \pm 1.551$, $t_{59} = -2.022$, $P = 0.048$). In total, we recorded
164 183.04 hours of video data (N = 62 videos; one video = one observation; mean video length ± SD 2.95
165 ± 1.07, range = 1 - 5 hours) from 40 distinct, breeding jackdaw pairs across 40 different nest boxes (N
166 = 5 videos in 5 boxes at colony X; 27 videos in 15 boxes at Y; and 30 videos in 20 boxes at Z). All
167 observations were conducted in the morning (start time 0630 - 0930 hours) to minimise the confounding
168 effect of changing behavioural patterns throughout the day. We recorded a minimum of one video at
169 each nest during the middle of the nest building phase in April. In seven cases, we recorded more than
170 one video per pair per breeding season, and for 14 pairs, we recorded at least one video in each of 2018
171 and 2019. Boxes were monitored regularly throughout the breeding season to document lay date, clutch
172 size, and egg volume. Measures of egg length and width served to calculate egg volume (Troscianko,
173 2014). In all observations, jackdaws built a nest, and all but one pair (box Z28, 2018), which was displaced
174 by another pair, laid eggs.

175 ## Video analysis

176 We analysed videos in a randomised order with regards to 'year' and 'study site', using the software *BORIS*
177 version 7.5.1 (Friard & Gamba, 2016). Relevant behaviours were recorded as either "point events" or

178 "states" (to quantify the number or duration of events, respectively; see ethogram in Table 1) and the
179 identity and sex of each individual was determined from its unique colour ring combination. In a minority
180 of cases, rings were not visible in the video during a bird's visit to the nest box, so the individual's sex
181 was recorded as "unknown". When the sex was relevant for analyses, we excluded data from unknown
182 focal individuals. If vocalisations occurred when both members of a pair were in the nest box, we used
183 fine-scale body movement (e.g. of beak or thorax) to establish which individual was vocalising. We
184 analysed different types of vocalisations with distinct acoustic qualities separately because they may be
185 functionally different. We analysed "chatter", a distinctive sequence of repeated high pitch vocalisations,
186 separately from other calls (hereafter called "calls") as they may be functionally different.

187 **Table 1 | Ethogram of behaviours recorded.** Type denotes whether a behaviour was a point event (PE) or a
188 state event (SE) with a duration. Begging calls by females are included in the event "call".

Behaviour	Type	Description
In box	SE/PE	Bird visits the nest box (PE) and spends time in it (SE).
Build nest	SE	Moving and adjusting nest material using the beak.
Bring nest material	PE	Carrying objects (straw, twigs, etc.) when entering the nest box.
Removed nest material	PE	Removing objects when leaving the nest box.
Form cup	SE	Lying down and adjusting material to form the cup.
Modify nest material	SE	Changing the structure of nest material, e.g. by cutting twigs.
Vigilance	SE	Peeking outside the nest box.
Food sharing (♂)	PE	Male visits nest box and shares food with his mate.
Chatter	SE	Soft, high pitch vocalisations.
Call	PE	Bird makes a call.

189

190 ## Statistical analyses

191 Data were analysed in *R* version 4.0.2 (R Core Team, 2020). For all behavioural variables (N = 10), we
192 extracted raw total durations (states) and quantities (point events) per observation for each pair (in total)

193 and for both sexes separately. To standardise variables, we divided raw data (durations or counts) by the
194 observation length (in seconds), and multiplied state events by 100 (percentage of time) and point events
195 by 3600 (rate per hour). For each standardised behavioural variable, we calculated means and standard
196 deviations (denoted as mean ± SD henceforth) across pairs.

197 **General procedure: mixed models and repeatability analysis**

198 Mixed models

199 We analysed data with (generalised) linear mixed models (LMMs and GLMMs), using the packages *lme4*
200 (for LMMs) (Bates et al., 2015) and *glmmTMB* (for GLMMs) (Brooks et al., 2017). To formulate models,
201 we selected the dependent variable of interest (a behaviour or a fitness proxy) and one or more
202 biologically meaningful independent variable(s). We subsequently tested model assumptions such as
203 normality of residuals, homoscedasticity, error structure, dispersion, zero inflation, and influential
204 datapoints (Cook's distance), using diagnostic plots and tests implemented in *R* (LMMs) or in the package
205 *DHARMa* (GLMMs) (Hartig, 2019). To infer estimates and *P*-values, we used Wald tests in the package
206 *car* (Fox & Weisberg, 2011). All models included the variables 'year' (fixed effect), 'pair ID' (random
207 effect), and 'study site' (random effect) to account for temporal and spatial variation as well as pseudo-
208 replication. We had no specific a priori predictions as to the effects of the birds' age, but as it could
209 potentially influence behaviour and reproductive success, we initially included 'age' (in years) in analyses
210 as an additional fixed effect. If age did not appear to play an important role, we removed the variable
211 from analyses to avoid over-parametrisation and maximise statistical power. Observation-level random
212 effects (X. A. Harrison, 2014) and COM-Poisson error structures accounted for zero-inflation and
213 underdispersion, respectively.

214 Repeatability analysis

215 We calculated the repeatability of behaviours and fitness proxies in pairs for which repeated measures
216 were available (N = 16 pairs observed more than once within and/or across years), using the package
217 *rptR* (Stoffel et al., 2017). When quantifying repeatability of state events, we used Box-Cox
218 transformations (Sakia, 1992) to meet assumptions of Gaussian data.

219 **Sex differences in behaviour**

220 We could identify birds for 76.71 ± 30.48 percent of the time spent in the box. To quantify sex differences
221 in behaviour, we used a subset of behavioural data where the identity of the focal individual(s) was known
222 (N = 62 videos of 40 pairs; two cases were removed in analyses including vocal communication because
223 the microphones failed to record: box Y02, 2018 and box Z19, 2018). We investigated the time both
224 sexes invested in 'vigilance', 'nest building', 'being in the nest box', 'forming the cup', and 'chatter', using
225 separate LMMs, with the standardised response variables log-transformed to meet model assumptions
226 (West et al., 2014). We also examined whether either sex invested more time in 'vigilance' or 'nest
227 building' as response variables given that these were the most frequent behaviours in the nest box. Models
228 examining only vigilance as response terms also contained the 'number of days the video had been
229 recorded before the lay date' (covariate) to account for the potential influence the date may have on
230 behaviours. For instance, birds may reduce their effort closer to the lay date when the nest should be
231 completed. On the other hand, males could increase their vigilance closer to the lay date to guard the
232 female during her fertile period. 'Modification of material' was too rare to permit formal statistical
233 analysis. We also conducted separate GLMMs on rates of 'material brought', 'material removed', 'visits
234 to the nest box', and 'calls' (rounded to rates per hour and treated as count data) fitted as a response term.
235 In these analyses, 'sex' was the main predictor variable of interest, but we also modelled an interaction
236 between sex and age of each bird to examine whether sex differences may be age-dependent and also to
237 include age as a covariate potentially affecting behaviour.

238 **Nest building and reproductive success**

239 Dependent variables: reproductive parameters

240 To examine fitness correlates of behaviours, we separately analysed three different proxies for
241 reproductive success (Table 2). Firstly, we used the relative lay date of the first egg compared to the date
242 the first clutch was initiated per site. As colonial breeders, jackdaws breed within a relatively short time
243 period, and early layers may benefit from lower competition with other colony members. A second proxy
244 of reproductive success was the clutch size. Thirdly, we examined the volume of the first and the third

245 egg). Jackdaws lay an egg per day until the clutch is complete, and they show hatching asynchrony, with
246 the first egg being the one which is most likely to survive. The second egg has a relatively high probability
247 to survive as well, whereas the survival rate of the third egg is approximately 0.5. We did not analyse later
248 eggs as these rarely survive (Goumas et al., In prep.). One pair (box Z28, 2019) was excluded from these
249 analyses because it was displaced by another pair during nest construction so could not produce a clutch.
250 When analysing egg volume, we removed one pair (box Y21, 2019), which had been parasitised by a
251 conspecific female. Two pairs were removed when analysing the third egg volume as they only laid two
252 eggs (box Y16, 2019; box Z15, 2019).

253 **Table 2 | Reproductive parameters to study fitness correlates of behaviour.** "N" denotes the sample size
254 (number of videos and of pairs, respectively) used in the models (unless stated otherwise). To calculate mean,
255 standard deviation, and the range of parameters, the sample size was smaller compared to the numbers presented
256 in this table because seven pairs observed twice in one year were only considered once here.

Reproductive parameter	Definition	Error structure	N	Mean ± SD	Range (min. – max.)
Lay date	Day first egg laid (1 = first egg per site)	COM-Poisson	61 (39)	5.19 ± 2.92	1 - 14
Clutch size	Number of eggs laid in total	COM-Poisson	61 (39)	4.43 ± 0.87	2 - 6
Egg volume	Egg volume of first egg (cm^3)	Gaussian	60 (38)	11.42 ± 0.85	9.75 - 13.19
Egg volume	Egg volume of third egg (cm^3)	Gaussian	58 (36)	11.23 ± 1.08	8.62 - 13.35

257

258 Behavioural predictors

259 We defined four 'behavioural concepts' to be used separately as independent variables that may relate to
260 measures of reproductive success. For each of the first three concepts we calculated a distinct PCA to
261 summarise (scaled) behavioural variables to be included in models whilst minimising model complexity
262 (Budaev, 2010; Morton & Altschul, 2019) and to account for multicollinearity among variables (Graham,
263 2003). When performing a PCA, we calculated a correlation matrix including the variables of interest,
264 applied the KMO-measure (threshold 0.5) to test for sufficient correlation among them (Budaev, 2010),

265 and conducted a parallel analysis to determine the number of principal components to be considered
266 objectively (Morton & Altschul, 2019), using the package *psych* (Revelle, 2018). We constructed alternative
267 models in cases where we analysed distinct predictors each of which reflected a specific hypotheses (for
268 more details see below). To select a model, we employed Akaike's Information Criterion (*AICc* to account
269 for small sample sizes (X. A. Harrison et al., 2018)) in the package *bbmle* (Bolker & R Core Team, 2017).
270 A model with the lowest *AICc* had to differ at least 2 *AICc* units to be selected. In instances where only
271 one predictor variable corresponded to one of the behavioural concepts, we did not use model selection
272 and constructed a single model per fitness variable instead. When we detected a significant relationship
273 between behavioural predictors and a fitness proxy, we performed models again with a subset of
274 observations for which data on female body condition was available in that particular year to control for
275 this variable (covariate). We then compared two models with and without female body condition using
276 likelihood ratio tests. Body condition was quantified using the residuals of a regression examining the
277 relationship between measures of body size (tarsus and wing length) as independent and body weight as
278 dependent variables. In all models investigating fitness correlates of behaviour, we also included the
279 'number of days the video was recorded before the lay date' ('day' henceforth, covariate), because this
280 could have influenced the birds' behaviour. Moreover, we fitted 'female age' (covariate) to account for
281 breeding experience (female and male age was significantly correlated: $\rho = 0.744$, $t_{59} = 8.560$, $P < 0.001$).
282 Another covariate was 'food sharing' by males, because this cooperative behaviour not directly related to
283 nest building could affect reproductive success. We outline each concept, and the analytical methods used
284 to examine it, below.

285 (i) Overall activity levels and intensity of behaviours

286 To test prediction 3 that pairs investing more in the nest relative to other activities, such as vigilance,
287 should lay earlier, and have larger clutches and eggs, we constructed a PCA of nine behavioural variables
288 ('PCA_{All}')(Table 3; Table A 4). The variable 'food sharing' (rate per hour) was left out in the PCA due to
289 the KMO-threshold (0.43), but included in the models as a covariate as levels of food sharing by the male
290 could influence the female's ability to invest in the nest and the clutch. All behavioural variables loaded

291 negatively onto $PC1_{All}$, which could therefore reflect 'intensity' of behaviours. The four nest building
292 behaviours loaded negatively onto $PC2_{All}$, whereas the other behaviours (vigilance, vocalisations, time in
293 the box) loaded positively onto $PC2_{All}$. These opposite loadings suggest a trade-off, such that pairs may
294 have invested relatively more time in either the nest or in vigilance and vocalising on the other. Therefore,
295 we hypothesised that (i) all behaviours ($PC1_{All}$), (ii) a relative investment in nest building compared to
296 other behaviours ($PC2_{All}$), or (iii) both ($PC1_{All}$ and $PC2_{All}$) could be used as predictor of reproductive
297 success. We formulated three corresponding models and two further models which contained (iv) only
298 'year' and 'day' and (v) only an 'intercept'. Subsequently, we compared these models using AICc.

299 (ii) Direct investment in the nest ('effort')

300 To examine prediction 4, we analysed the relationship between a PCA comprising variables directly
301 related to nest building and reproductive success ('$PC1_{Effort}$'; Table 3; Table A 5). All four variables loaded
302 negatively onto '$PC1_{Effort}$', suggesting it could be used as a measure of total nest building effort. Following
303 the parallel analysis that quantified the number of principal components to be used, we constructed only
304 one model per fitness proxy, including '$PC1_{Effort}$' as an independent variable instead of comparing
305 alternative models.

306 (iii) Relative investment by females in nest building and vigilance ('division of labour', 'DoL')

307 We conducted a third PCA to examine 'division of labour' ('DoL') (prediction 5), that is, whether the
308 relative proportion of female contribution to nest building and vigilance (compared to the sum of female
309 and male effort) was linked to reproductive success ('PCA_{DoL}'; Table 3; Table A 6). In this analysis, the
310 sample size was smaller (N = 47 observations), because we discarded observations when a proportion
311 could not be calculated (neither sex of a pair showed one of the behaviours). $PC1_{DoL}$ suggested that
312 females contributed either more through nest building or vigilance due to opposite loadings (Table A 6).
313 $PC2_{DoL}$ was equivalent to the 'relative proportion of material brought by females' (loading = 0.99; Table
314 A 6). When analysing 'PCA_{DoL}', we constructed alternative models per fitness proxy by using either (i)
315 '$PC1_{DoL}$', (ii) the 'relative proportion of material brought by females', (iii) only 'year' and 'day', or (iv) only

316 an 'intercept' as independent variables. For predictors (i) and (ii) we also modelled a quadratic effect
317 which could indicate that equal contributions by both sexes are related to greater reproductive success.

318 (iv) Time spent together in the nest box ('synchrony')

319 To test prediction 6 that the level of 'synchrony' could be linked to reproductive success, we used the
320 'proportion of time individuals spent together in the nest box' as an independent variable. To examine
321 its relationship with fitness measures, we constructed one model per fitness proxy with 'synchrony' being
322 the only independent variable.

323 **Table 3| Behavioural concepts used to examine correlates of reproductive success.** The two sample sizes
324 denote the number of observations and the number of pairs, respectively. In the PCA_{All}, the variables 'food sharing'
325 (KMO = 0.46) and 'modify' (rare behaviour) were left out. $PC2_{DoL}$ was equivalent to 'material brought' by females
326 (loading 0.99) and therefore the latter variable was used. For more details on the PCA please refer to the Appendix.

Behavioural concept	**Definition**	**Predictor variables in models (standardised by observation length)**
PCA_{All} (N = 59; 39)	Intensity of behaviours: nest building, vigilance, time in the box, vocalisation	$PC1_{All}$ and $PC2_{All}$ ('nest building', 'material brought', 'material removed', 'forming the cup', 'vigilance', 'chatter', 'calls', 'together in the nest box', 'box occupied')
Effort (PCA_{Effort}; N = 61; 39)	Direct investment in nest building activities	$PC1_{Effort}$ ('nest building', 'material brought', 'material removed', 'forming the cup')
Division of labour (PCA_{DoL}; N = 47; 34)	Relative contribution by females to cumulative time investment in nest building and vigilance ('division of labour')	$PC1_{DoL}$ and $PC2_{DoL}$ (relative proportion of 'nest building', 'material brought', and 'vigilance' by females)

Synchrony (N = 61; 39)	Visits and time in the box matched by both birds	'Together in the nest box'

3. Results

Behaviours and sex differences

Sex differences

On average, jackdaw pairs occupied their nest box for 29.09 ± 19.64 percent of the observations and spent 23.17 ± 24.58 percent of that time together. The behavioural repertoire of both sexes was broadly similar (Figure 1), but they also differed in some behaviours (Figure 2, Table 4). Specifically, females spent 1.5 times more time building the nest than males (Figure 2a, Table 4). Males spent on average 1.4 times more time being vigilant than females, but this difference was not significant (Figure 2b, Table 4). Moreover, males spent more time being vigilant than they spent building, whilst females were similar in both behaviours (Table 4). Males did not increase vigilance when the observation was recorded closer to the lay date (LMM, sex * days before lay date: β ± SE = 0.021 ± 0.023, X^2_1= 0.887, 95 % CI [- 0.01, 0.03], P = 0.346). Females called 1.9 times more frequently than males (Figure 2c, Table 4), even after removing female begging calls (GLMM, sex: β ± SE = - 0.690 ± 0.228, X^2_1= 9.120, P = 0.003). There was weak evidence that older birds brought more nesting material (GLMM, sex: sex: β ± SE = 0.257 ± 0.124, X^2_1= 4.135, 95 % CI [0.013, 0.500], P = 0.042; Figure A 1), but this relationship was not maintained when removing the four youngest individuals that were two years old (GLMM, age: β ± SE = 0.177 ± 0.127, X^2_1= 1.645, 95 % CI [- 0.073, 0.426], P = 0.200). Aside from this there was no evidence for any age effects or sex by age interactions on any aspect of building behaviour (Table A 3).

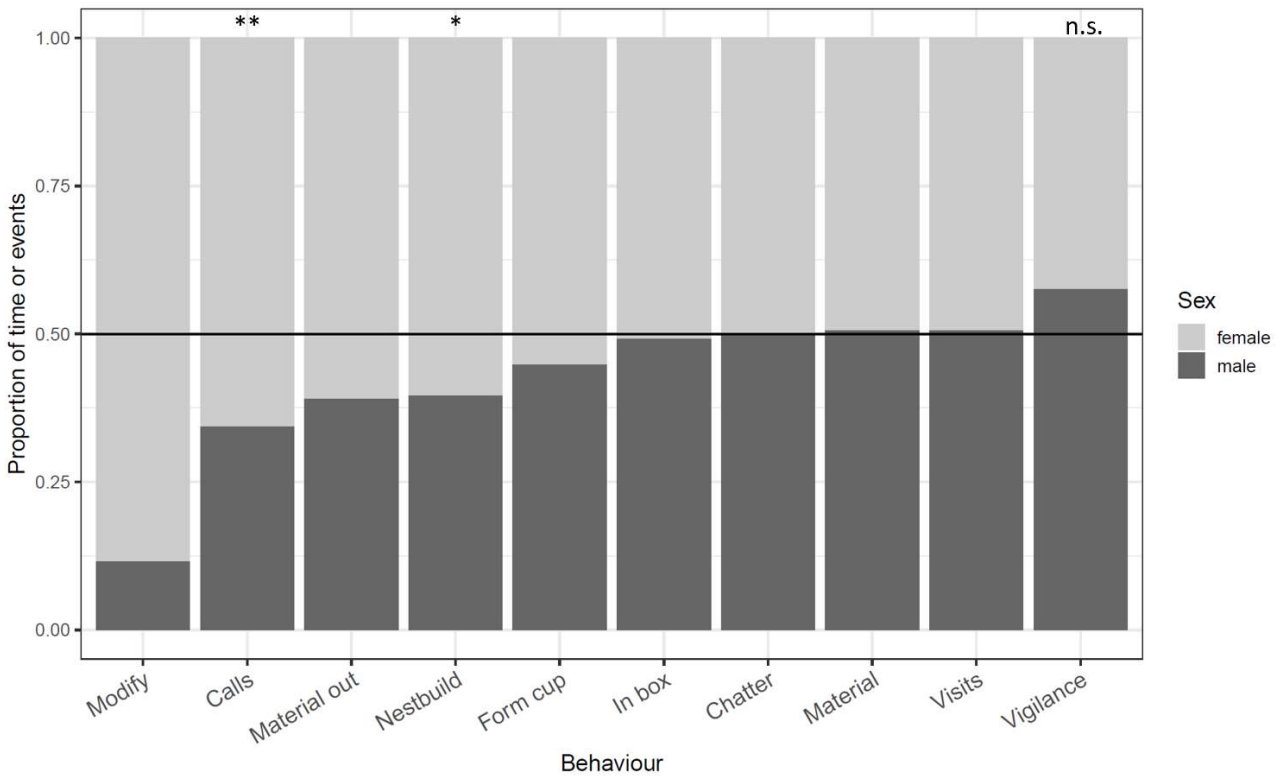


Figure 1 | Mean relative duration (state events) and frequency of events (point events) by sex (N = 62 observations; N = 60 for vocalisations). The horizontal line marks the proportion of 0.5, meaning both sexes showed a behaviour equally long or often, respectively. Asterisks indicate a significant sex difference in behaviour based on the model output (calls, nest building; < 0.01 ** and < 0.05 *).

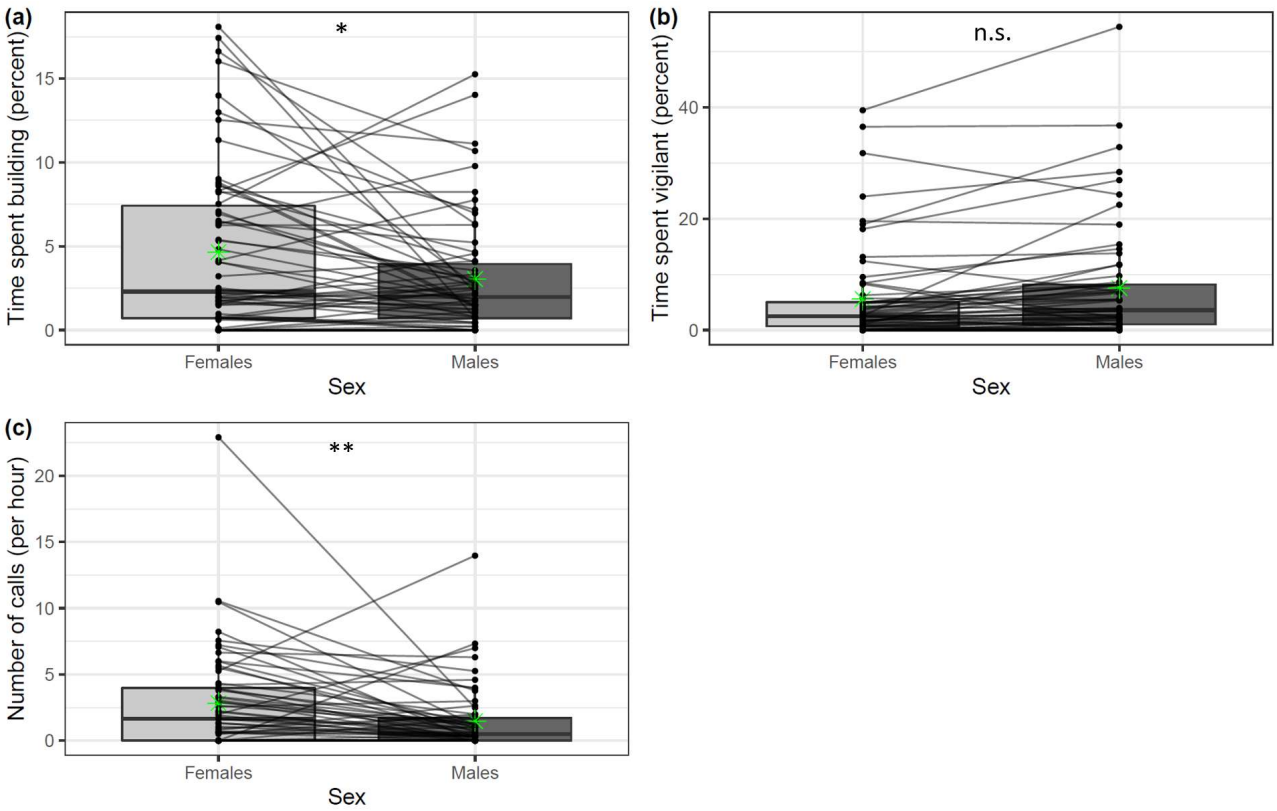


Figure 2 | Sex differences in three behavioural variables (N = 62 observations; N = 60 for calls). Horizontal lines in the boxes indicate the median, green asterisks indicate the mean. Upper and lower ends of the boxes reflect the 0.25 and the 0.75 quartiles, respectively. Horizontal lines connecting points represent distinct pairs. Asterisks indicate a significant difference (** < 0.01; * < 0.05; n.s. = 0.060). **(a)** The time spent building the nest as a percentage of the observation length. **(b)** The time spent being vigilant as a percentage of the observation length. **(c)** The number of calls made by both sexes (per hour).

362 **Table 4 | Sex differences in behaviour.** Statistically significant results are in bold. Response variables for LMMs
363 were log-transformed and estimates for GLMMs (COM-Poisson) are on the log scale. Intercepts refer to the values
364 of females and to the year 2018. Observation-level random effects accounted for zero-inflation. σ^2 and σ denote
365 the variation and standard deviation attributed to random effects. Sex differences were not examined for rarer
366 behaviours (modification of nest material).

Response variable (model)	**Fixed effects**	**β**	**SE (β)**	***X²***	**df**	**95 % CI (lower)**	**95 % CI (upper)**	***P***
In box (LMM)	Intercept	2.682	0.183		1			
	Sex	0.017	0.162	0.011	1	- 0.301	0.335	0.916
	Year	- 1.003	0.191	27.579	1	- 1.376	- 0.630	**< 0.001**
Random effects: Pair ID (σ^2, σ) = 0.498, 0.706; Site (σ^2, σ) = 0.000, 0.000								
Build nest (LMM)	Intercept	1.603	0.130		1			
	Sex	- 0.237	0.112	4.522	1	- 0.457	- 0.018	**0.033**
	Year	- 0.580	0.133	19.008	1	- 0.845	- 0.319	**< 0.001**
Random effects: Pair ID (σ^2, σ) = 0.271, 0.520; Site (σ^2, σ) = 0.000, 0.000								
Vigilance (LMM)	Intercept	1.591	0.161		1			
	Sex	0.259	0.138	3.520	1	- 0.012	0.530	0.060
	Year	- 0.787	0.165	22.795	1	- 1.109	- 0.464	**< 0.001**
Random effects: Pair ID (σ^2, σ) = 0.423, 0.650; Site (σ^2, σ) = 0.000, 0.000								

Build vs. vigilance (LMM)	Intercept	1.607	0.138		1			
	Sex	- 0.237	0.133	0.013	1	- 0.498	0.023	0.909
	Behaviour	- 0.025	0.133	5.590	1	- 0.286	0.235	**0.018**
	Sex * Behaviour	0.497	0.189	6.924	1	0.128	0.865	**0.009**
	Year	- 0.678	0.116	34.267	1	- 0.904	- 0.453	**< 0.001**

Random effects: Pair ID (σ^2, σ) = 0.292, 0.540; Site (σ^2, σ) = 0.000, 0.000

Visits (GLMM)	Intercept	1.567	0.130		1			
	Sex	0.001	0.121	0.000	1	- 0.237	0.238	0.995
	Year	- 0.995	0.162	37.655	1	- 1.313	- 0.677	**< 0.001**

Random effects: Pair ID (σ^2, σ) = 0.212; 0.461, Site (σ^2, σ) = 0.000, 0.000

Material (GLMM)	Intercept	0.855	0.197		1			
	Sex	0.513	0.716	0.046	1	- 0.889	1.916	0.830
	Age	0.257	0.124	4.135	1	0.013	0.500	**0.042**
	Sex * Age	- 0.108	0.134	0.650	1	- 0.372	0.155	0.420
	Year	- 1.589	0.289	30.311	1	- 2.154	- 1.023	**< 0.001**

Random effects: Pair ID (σ^2, σ) = 0.405, 0.636; Site (σ^2, σ) = 0.000, 0.000

Material out	Intercept	- 1.560	0.483		1			
	Sex	- 0.390	0.480	0.658	1	- 1.331	0.552	0.417

(GLMM)	Year	- 1.080	0.514	4.422	1	- 2.087	- 0.073	**0.035**
Random effects: Pair ID (σ^2, σ) = < 0.001, < 0.001; Site (σ^2, σ) = 0.000, 0.000								
Form cup (LMM)	Intercept	0.607	0.061		1			
	Sex	- 0.061	0.053	1.340	1	- 0.165	0.042	0.247
	Year	- 0.320	0.063	25.843	1	- 0.443	- 0.197	**< 0.001**
Random effects: Pair ID (σ^2, σ) = 0.062, 0.248; Site (σ^2, σ) = 0.000, 0.000								
Chatter (LMM)	Intercept	0.296	0.051		1			
	Sex	0.006	0.052	0.015	1	- 0.095	0.108	0.901
	Year	- 0.222	0.057	15.046	1	- 0.333	- 0.110	**< 0.001**
Random effects: Pair ID (σ^2, σ) = 0.022, 0.147; Site (σ^2, σ) = 0.000, 0.000								
Calls (GLMM)	Intercept	1.026	0.239		1			
	Sex	- 0.717	0.233	9.466	1	- 1.175	- 0.261	**0.002**
	Year	- 0.582	0.276	4.467	1	- 1.122	- 0.042	**0.035**
Random effects: Pair ID (σ^2, σ) = 0.001, 0.026; Site (σ^2, σ) = 0.000, 0.000								

Repeatability and variation across pairs and years

There was considerable variation in behaviours between different pairs (Figure 2; Table A 1; Table A 2), but when inside the nest box, the majority of their time was spent building the nest or being vigilant (Table A 1). On the level of the pair, birds that spent more of their time in the nest box together spent more time being vigilant (ϱ = 0.906, t_{60} = 16.547, P < 0.001), but not more time building (ϱ = 0.139, t_{60}

373 = 1.090, P = 0.280). Conversely, pairs in which only one individual occupied the nest box for longer
374 spent more time building (ϱ = 0.840, t_{60} = 11.996, P < 0.001), but not more time being vigilant (ϱ = 0.175,
375 t_{60} = 1.379, P = 0.173). The time females spent building and males spent being vigilant was positively
376 correlated (ϱ = 0.271, t_{60} = 2.184, P = 0.033). No behaviour was repeatable in 16 pairs for which repeated
377 measures were available within and/or between years (Table A 8). Jackdaws varied in their behaviour
378 depending on the year (Table 4).

379 Behaviours and correlates of reproductive success

380 The volume of the first egg (R = 0.598 ± 0.176, 95 % CI [0.182, - 0.850], P = 0.009) and the third egg (R
381 = 0.598 ± 0.187, 95 % CI [0.115, - 0.848], P = 0.007) females laid was repeatable across years. The relative
382 lay date of pairs compared to the first lay date per site was also repeatable (R = 0.643 ± 0.204, 95 % CI
383 [0.018, - 0.822], P = 0.015). Clutch size was not repeatable for those pairs observed in both years (Table
384 A 9).

385 **Lay date**

386 The majority of jackdaw females laid their first egg in the middle of April (17.05 ± 3.20 days where 1 =
387 1st April; 5.19 ± 2.92 days after the first clutch was initiated per site). Females that laid their first egg
388 relatively earlier contributed relatively more to bringing material (Figure 3; Table 5). In this model, female
389 age did not appear to have an effect and was therefore removed (β ± SE = 0.086 ± 0.082, X^2_1= 1.108, P
390 = 0.292, 95 % CI [- 0.074, 0.246]). Including a proxy for female body condition did not improve the
391 model (X^2_1 < 0.001, P = 1.0).

392

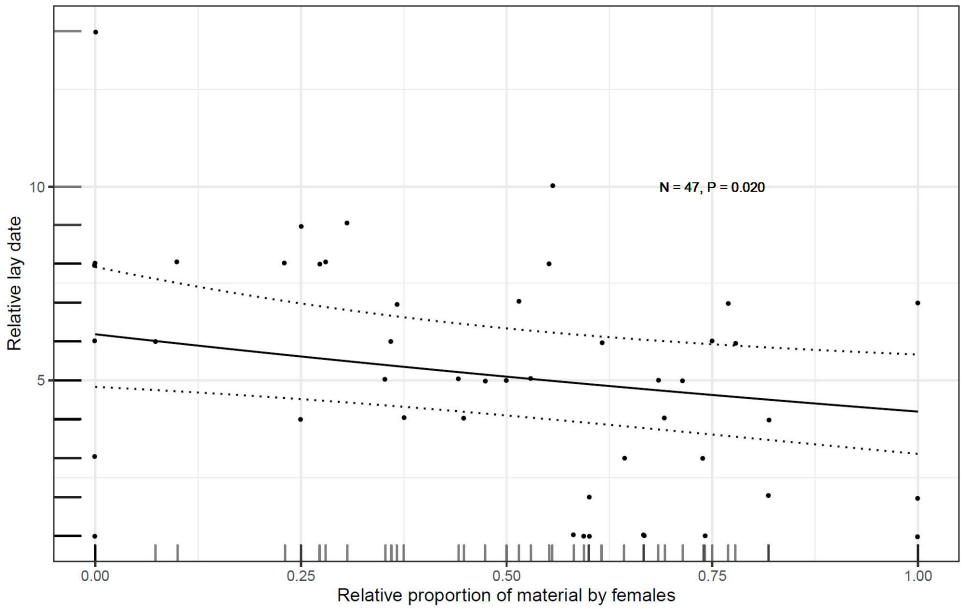


Figure 3 | Relationship between the relative lay date (number of days compared to the day the first clutch was initiated per site) and female contribution to transporting nest material to the nest box. The relative proportion of items brought by females refers to the total amount of nest material brought by females and males. Dots indicate raw data; dotted lines show the 95 % confidence intervals around the fitted line (solid) from the model output.

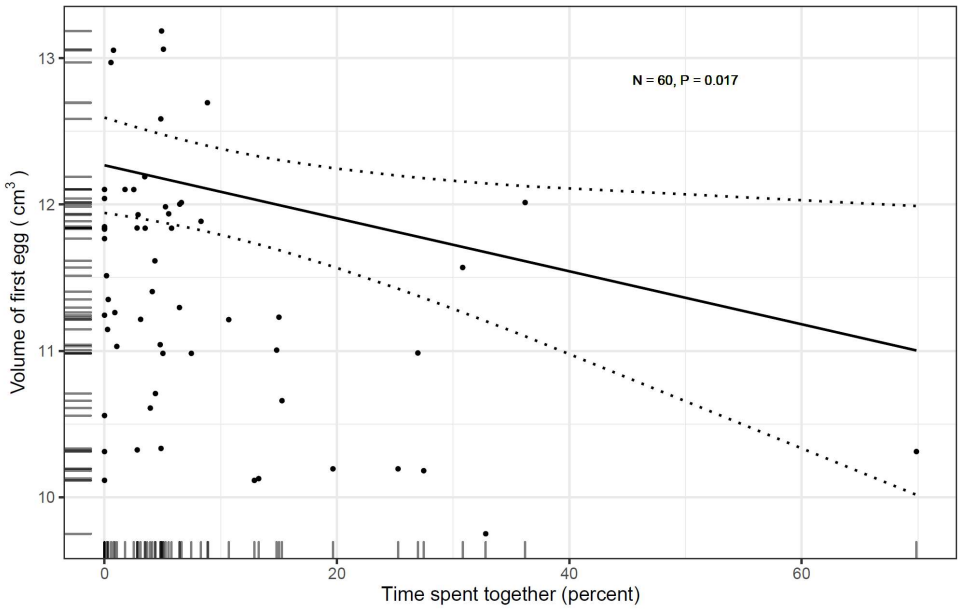
Clutch size

Females laid a mean of 4.43 ± 0.87 eggs. Clutch size was unrelated to any of the behavioural predictors (Table A 7).

Egg volume

The mean volume of the first and the third egg was 11.42 ± 0.85 cm^3 and 11.23 ± 1.07 cm^3, respectively. The volume of both the first and the third egg was smaller in birds that spent more time together in the box (Figure 4; Table 5). This relationship remained after excluding an influential datapoint (a pair that spent more than 60 % of the time together in the nest box) (LMM, synchrony, first egg: β ± SE = - 0.027 ± 0.012, X^2_1= 5.590, P = 0.018, 95 % CI [- 0.051, - 0.003]; third egg: β ± SE = - 0.046 ± 0.014, X^2_1= 10.648, P = 0.001, 95 % CI [- 0.075, - 0.016]). In the models examining synchrony there was no effect of female age on egg volume (LMM, age, first egg: β ± SE = 0.102 ± 0.094, X^2_1= 1.169, P = 0.280, 95 % CI [- 0.076, 0.290]; third egg: β ± SE = 0.005 ± 0.115, X^2_1= 0.002, P = 0.962, 95 % CI [- 0.212, 0.228].

411 Including female body condition did not improve the model examining the relationship between
412 synchrony and first egg volume (X^2_1 0.113, $P = 0.945$), and between synchrony and third egg volume (X^2_1
413 0.013, $P = 0.909$).



414

415 **Figure 4 | Relationship between the first egg volume per female and the percentage of time mates spent**
416 **together in the nest box.** The continuous fitted line corresponds to the model output; dotted lines show the 95
417 % confidence intervals. The result was still significant when excluding an outlier (a pair spending more than 60 %
418 of the time together in the box).

419

420 **Table 5 | Summary of the statistical analyses on the relationship between behaviours at the nest building**
421 **phase and fitness proxies.** The fixed effect 'Material (♀)' reflects the relative female contribution to bringing
422 nest material relative to the overall effort by both sexes. The reference year was 2018 and 'day' refers to the number
423 of days the video was recorded before the lay date of the first egg. σ^2 and σ show the variation and standard
424 deviation explained by random effects. This table shows significant results; further details are in the Appendix
425 (Table A 7).

Response variable (model)	Fixed effects	β	SE (β)	X^2	df	95 % CI (lower)	95 % CI (upper)	*P*

Relative lay date (GLMM)	Intercept	1.168	0.415		1			
	Material (♀)	- 0.388	0.167	5.395	1	- 0.715	- 0.061	**0.020**
	Food sharing (♂)	- 0.546	0.299	3.330	1	- 1.131	0.040	0.068
	Year	- 0.124	0.126	0.983	1	- 0.371	0.122	0.322
	Day	0.020	0.007	8.140	1	0.006	0.034	**0.004**
	Random effect: Pair ID (σ^2, σ) = 0.318, 0.564; Site (σ^2, σ) < 0.001, < 0.001							
Volume of first egg (LMM)	Intercept	11.814	0.249		1			
	Synchrony	- 0.019	0.008	5.793	1	- 0.034	- 0.004	**0.016**
	Food sharing (♂)	0.746	0.592	1.587	1	- 0.418	1.889	0.282
	Year	- 0.329	0.186	3.118	1	- 0.685	0.026	0.077
	Day	0.034	0.017	4.145	1	0.002	0.066	**0.042**
	Random effect: Pair ID (σ^2, σ) = 0.347, 0.589; Site (σ^2, σ) < 0.001, < 0.001							
Volume of third egg (LMM)	Intercept	11.291	0.578		1			
	Synchrony	- 0.027	0.010	7.486	1	- 0.048	- 0.007	**0.006**
	Food sharing (♂)	0.061	0.747	0.008	1	- 1.330	1.464	0.929
	Year	- 0.211	0.282	0.557	1	- 0.663	0.243	0.455
	Day	0.023	0.021	1.236	1	- 0.016	0.063	0.266
	Random effect: Pair ID (σ^2, σ) = 0.450, 0.671 ; Site (σ^2, σ) < 0.001, < 0.001							

Discussion

Our findings demonstrate that in monogamous jackdaws nest building entails substantial investment from both partners, and may have important fitness consequences. Although both sexes exhibited a similar behavioural repertoire and cooperated to create their nest, there were some sex differences in investment, with females building more and males tending to be more vigilant. Moreover, some aspects of behaviour, such as the relative female contribution to transporting material and time spent together in the box, were associated with measures of reproductive success (lay date and egg volume).

Consistent with our predictions, jackdaws cooperated during nest construction, with the two sexes behaving broadly similarly, with both investing in bringing material, building the nest, and forming the cup. In jackdaw pairs fitness outcomes are interdependent due to repeated mating opportunities with the same partner across years and low rates of divorce and successful extra-pair copulations (Gill et al., 2020; Wechsler, 1989). Under these circumstances, conflicts of interest between mates may be minimised, particularly if biparental care is necessary to successfully rear offspring, ultimately favouring cooperation. Although nest building by jackdaws clearly requires a substantial cooperative investment from both partners, our findings suggest moderate division of labour could facilitate cooperation (cf. Iserbyt, Fresneau, Kortenhoff, Eens, & Müller, 2017). Females built more than males and were therefore more responsible for the nest structure. In contrast, males dedicated more time to vigilance than to building, which may be particularly important in colonially nesting jackdaws, where intraspecific competition over nest cavities is severe and can constrain reproduction (Henderson & Hart, 1993; Röell, 1978; Verhulst & Salomons, 2004). Vigilant residents may not only anticipate threatening non-resident competitors searching for a nest cavity, but their bright eye colour has also been shown to deter intruders (Davidson et al., 2014). Males may prioritise vigilance because the risks of vigilance and defence may be more costly for females as they need to stay in a good condition for later stages of breeding, such as incubation. Additionally, males may invest relatively more in vigilance than in building due to their slightly larger body size (Fletcher & Foster, 2010), a trait which impacts contests in this species (Verhulst et al., 2014). There was no significant difference in the amount of time males and females spent in vigilance, and male

458 vigilance was independent of days until his partner's fertile window (beginning 5 days prior to the lay
459 date; Gill et al., 2020), suggesting that vigilance serves primarily to defend the nest site rather than as a
460 form of mate-guarding. Males cooperated, for example through vigilance and transporting nest material
461 despite contributing less to building the nest by arranging material in the nest box. By increasing their
462 own nest building activity, females may be able to partially compensate for this. Females may also spend
463 more time building than males because they may be better informed about their own requirements for
464 incubating the clutch. The mechanisms through which partners acquire and act upon information to
465 respond to each other's behaviour and coordinate division of labour remains unknown. Elucidating these
466 mechanisms will be vital to understanding the cognitive demands of pair-bonding, such as the need to
467 track and respond to another's behaviour (Emery et al., 2007).

468 Our results suggest substantial variation in behaviour and time budgets between pairs. Furthermore, no
469 behavioural variable was significantly repeatable within pairs, indicating there may also be considerable
470 behavioural variation within pairs. It is possible that the lack of repeatability within pairs is an artefact of
471 differences in sampling between years, because videos were recorded significantly closer to the lay date
472 in 2019, which could have affected the behaviour. For instance, pairs may have seemingly built less in
473 2019, but this could have been because the video was recorded closer to the lay date. Given the limited
474 amount of data per pair and the fact that not all pairs were observed repeatedly, these results must be
475 interpreted with caution. Nevertheless, our findings raise the possibility that there may be substantial
476 phenotypic plasticity in jackdaw nest building behaviour, in keeping with recent evidence nest building
477 behaviour may be less 'fixed' than previously thought (Walsh et al., 2013). Indeed, we found intensity of
478 behaviours significantly varied across two years, implying that environmental variables may affect
479 behaviour, and also measures of reproductive success.

480 Some behaviours during nest construction were associated with proxies for reproductive success, raising
481 the possibility that selection pressures may act on how pairs cooperate and how they spend their time.
482 The relative contribution of females to bringing nest material was associated with an earlier lay date.
483 Given that early laying can reduce competition for food when provisioning offspring and is often linked

484 to elevated reproductive success in birds (Perrins, 1970), this suggests the female contribution to nest
485 building may have important fitness consequences. We had hypothesised that more equal contributions
486 by both partners could enable an earlier lay date by reducing the time and energy needed to build the
487 nest, potentially important for females to save energy for costly egg production (Williams, 2005). Instead,
488 we found that the time females spent building and males spent being vigilant was positively correlated,
489 suggesting that greater investment in vigilance by the male may allow the female to invest more energy
490 in building the nest and thus lay earlier.

491 The amount of time partners spent together was also linked to fitness outcomes, but in the opposite
492 direction to our predictions. Whereas we had predicted that greater synchrony would reflect compatibility
493 between partners and be linked to reproductive benefits (Spoon et al., 2006), we actually found more
494 synchronous pairs laid smaller eggs. One possible explanation for this is that the pairs that spent more
495 time together in the nest were those that faced greater competition, as both partners are required to
496 successfully guard a nest site in this species (Röell, 1978; Verhulst & Salomons, 2004). Indeed, we found
497 that pairs that spent more time together invested more time in vigilance but not in building the nest. This
498 suggests a competitive and stressful period where the need to defend the nest box detracts from
499 investment in nest building (Röell, 1978). There is evidence from other species, such as house sparrows
500 (*Passer domesticus*), that investment in parental care, and consequent reproductive success, can be impaired
501 by chronically elevated stress hormone levels (Ouyang et al., 2011). While including morphological
502 measures of female body condition did not improve our models, measures of current energetic and
503 physiological state may prove more useful in future studies.

504 Together, our findings indicate that nest building in monogamous birds provides an important, but as
505 yet understudied, model system to investigate the evolution and proximate mechanisms of cooperation.
506 How much a partner invests in nest building may be a source of information used by individual birds to
507 assess how much their partner could be willing to invest later on during the breeding attempt. This may
508 be critical for individuals to estimate and to adjust their own effort. In the future, finer-scale analyses may
509 also allow us to understand whether and how individuals respond strategically to each other's behaviour,

for example by taking turns (cf. Johnstone & Savage, 2019; Savage et al., 2017). Given growing evidence that nest building improves with experience (Muth & Healy, 2011), it is also important to establish whether pairs learn and refine their cooperative nest building strategies over time. Although there was little evidence that age was an important factor in our analyses, future work will be vital to determine whether and how the prior history of specific partners shapes their behaviour and reproductive success. Finally, investigations of nest building may also contribute to our understanding of animal architecture. To date, the majority of research on cooperative architecture has focused on the nests and mounds of eusocial insects, where the colony is the unit of reproduction. Cooperative nest-building in birds may provide useful opportunities to understand how variation in conflicts of interest influences the adaptive value of cooperating to build structures for mutual benefit, and the proximate mechanisms through which this is achieved.

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Appendix

i. Behavioural variables

Table A 1 | Behaviours (state events) jackdaws showed in their nest box (N = 62 observations; N = 60 for chatter). The second and third column summarise the percentage of time pairs showed each behaviour. The subsequent two columns indicate the amount of time (percentage of observation length) both sexes exhibited a particular behaviour. The behaviours of the sexes do not always add up to the cumulative amount because in some instances a bird was not identifiable.

Behaviour	Percent of time (out of obs. length) Mean ± SD	Percent of time (out of time in box) Mean ± SD	Females ♀: percent of time (obs. length) Mean ± SD	Males ♂: percent of time (obs. length) Mean ± SD
In box (cum.)	37.96 ± 30.50	-	**16.06 ± 15.99**	**15.50 ± 15.04**
Box occupied	29.09 ± 19.64	-	-	-
In box (both)	8.99 ± 13.56	23.17 ± 24.58	-	-
Vigilance	15.73 ± 19.24	37.83 ± 19.32	5.58 ± 8.69	**7.57 ± 10.47**
Build nest	9.59 ± 8.39	27.34 ± 16.92	**4.66 ± 4.95**	3.05 ± 3.48
Form cup	1.67 ± 1.70	4.71 ± 4.01	0.74 ± 0.90	0.60 ± 0.68
Modify	0.05 ± 0.13	0.15 ± 0.52	0.024 ± 0.075	0.003 ± 0.014
Chatter	0.92 ± 1.70	1.93 ± 2.50	0.33 ± 0.80	0.33 ± 0.77

Table A 2| Behaviours (point events) shown by jackdaw pairs (N = 62 observations). The second and third column describe the total number of events per observation and per hour, respectively. The last two columns summarise the number of events per hour for both sexes separately. Please note the behaviours of the sexes do not add up to the cumulative amount, as individuals were sometimes unidentifiable.

Behaviour	Number of events per	Number of events per hour Mean ± SD	Females ♀: number of events per hour	Males ♂: number of events per hour

	observation Mean ± SD		Mean ± SD	Mean ± SD
Visits	32.53 ± 28.01	10.06 ± 8.07	3.71 ± 3.13	3.80 ± 3.87
Material	18.89 ± 20.99	5.71 ± 6.09	2.12 ± 2.42	2.17 ± 3.42
Material out	4.68 ± 7.93	1.44 ± 2.46	0.67 ± 1.42	0.43 ± 0.95
Calls	18.05 ± 23.85	5.52 ± 5.85	**2.83 ± 3.84**	1.48 ± 2.45
Food sharing (♂)	0.27 ± 0.48	0.09 ± 0.18	-	0.09 ± 0.18

Table A 3 | Relationship between behaviours shown by jackdaws and age.

Response variable (model)	**Fixed effects**	**β**	**SE (β)**	***X²***	**df**	**95 % CI (lower)**	**95 % CI (upper)**	***P***
In box (LMM)	Age	0.091	0.112	0.398	1	- 0.127	0.310	0.528
	Sex * Age	- 0.059	0.116	0.264	1	- 0.285	0.165	0.607
Build nest (LMM)	Age	0.054	0.079	0.573	1	- 0.100	0.208	0.449
	Sex * Age	- 0.011	0.080	0.017	1	- 0.166	0.145	0.895
Vigilance (LMM)	Age	0.050	0.099	0.036	1	- 0.140	0.241	0.849
	Sex * Age	- 0.060	0.099	0.367	1	- 0.251	0.132	0.545
Build vs. vigilance (LMM)	Age	0.027	0.059	0.205	1	- 0.088	0.141	0.651

Visits	Age	0.165	0.081	2.380	1	0.005	0.324	0.123
(GLMM)	Sex * Age	- 0.111	0.085	1.712	1	- 0.278	0.055	0.191
Material out	Age	0.222	0.243	0.275	1	- 0.255	0.698	0.600
(GLMM)	Sex * Age	- 0.247	0.322	0.590	1	- 0.878	0.383	0.442
Form cup	Age	0.048	0.037	1.380	1	- 0.025	0.120	0.240
(LMM)	Sex * Age	- 0.022	0.038	0.347	1	- 0.096	0.051	0.556
Chatter	Age	0.059	0.032	2.112	1	- 0.002	0.121	0.146
(LMM)	Sex * Age	- 0.043	0.036	1.389	1	- 0.113	0.027	0.239
Calls	Age	- 0.044	0.148	1.046	1	- 0.334	0.247	0.306
(GLMM)	Sex * Age	0.280	0.169	2.378	1	- 0.051	0.611	0.098

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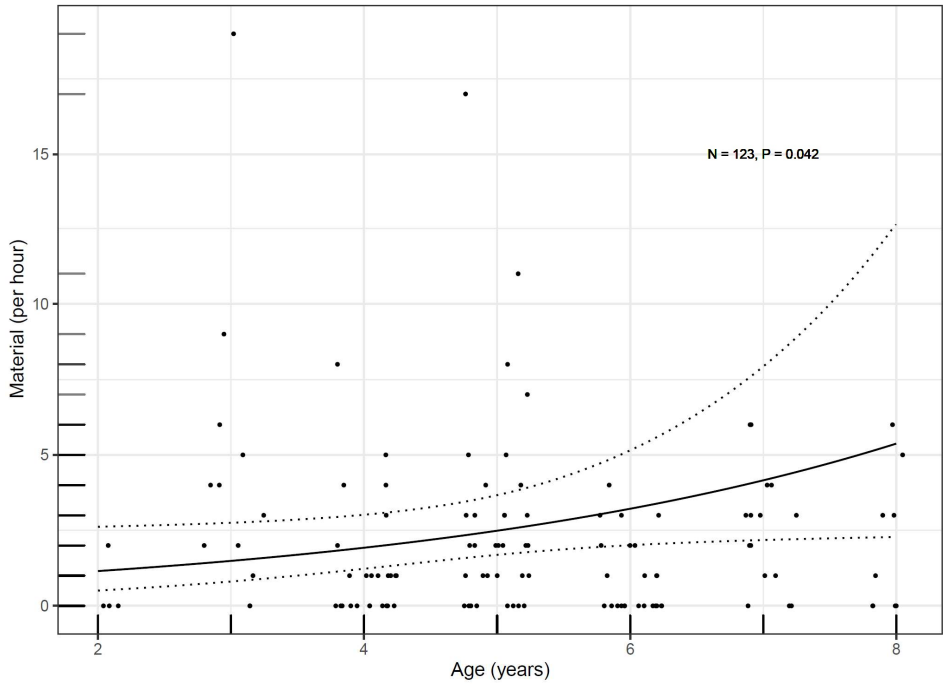

Figure A 1 | The number of material brought by individual birds (rounded, per hour) plotted against their age (horizontal jitter used to make datapoints more distinguishable). The relationship was non-significant when removing four individuals that were two years old ($P = 0.200$). The continuous fitted line corresponds to the model output; dotted lines show the 95 % confidence intervals.

ii. Fitness correlates: Principal Component Analyses (PCA)

Table A 4 | Loadings of behavioural variables onto the first two principal components of the PCA_{All} including nine different behaviours (N = 59).

Behaviour	PC1	PC2
In box (cumulative)	- 0.456	0.175
In box (both birds)	- 0.354	0.391
Build nest	- 0.344	- 0.385
Material	- 0.309	- 0.449
Material out	- 0.224	- 0.478
Form cup	- 0.266	- 0.226
Vigilance	- 0.380	0.390

Chatter	- 0.297	0.048
Calls	- 0.317	0.180
Variation explained	46.54	25.22

Table A 5 | Loadings of behavioural variables related to nest building onto $PC1_{Efffort}$ and $PC2_{Efffort}$ of the $PCA_{Efffort}$ (N = 61).

Behaviour	**PC1**	**PC2**
Build nest	- 0.541	0.017
Material	- 0.543	- 0.123
Material out	- 0.496	- 0.558
Form cup	- 0.408	0.821
Variation explained	69.18	18.86

Table A 6 | Loadings of behavioural variables (relative female contribution) onto PC1 and PC2 of the PCA_{DoL} (N = 61).

Behaviour	**PC1**	**PC2**
Build nest ♀	0.700	- 0.118
Material ♀	0.116	0.992
Vigilance ♀	- 0.704	0.046
Variation explained	58.16	33.06

iii. Fitness correlates: mixed models

Table A 7 | Different models to examine the effect of behaviours on proxies for reproductive success. In all models we accounted for the 'year', 'day', 'food sharing' and 'female age' as fixed effects. 'Pair ID' and 'site' were included as random effects in all models. The column 'best model' shows which model had the lowest AICc in cases where we performed model selection. The last two columns show the estimate, standard error, and P-value for the instances where we did not use AICc but constructed single models.

Response variable	Concept (models)	Fixed effects	Error structure	Best model (Δ AICc)	β ± SE (β)	*P*
Relative lay date	PCA_{All} (5)	$PC1_{All}$, $PC2_{All}$	GLMM: COM-Poisson	Year, Day (3.3)	-	-
	PCA_{Effort} (1)	$PC1_{Effort}$		-	- 0.012 ± 0.012	0.286
	PCA_{DoL} (6)	$PC1_{DoL}$, Material by ♀		Material ♀ (4.7)	-	-
	Synchrony (1)	Together in box		-	0.002 ± 0.003	0.546
Clutch size	PCA_{All} (5)	$PC1_{All}$, $PC2_{All}$	GLMM: COM-Poisson	Null model (0.0)	-	-
	PCA_{Effort} (1)	$PC1_{Effort}$		-	0.005 ± 0.017	0.753
	PCA_{DoL} (6)	$PC1_{DoL}$, Material by ♀		Null model (3.6)	-	-
	Synchrony (1)	Together in box		-	- 0.002 ± 0.002	0.424
Volume of 1st egg	PCA_{All} (5)	$PC1_{All}$, $PC2_{All}$	LMM: Gaussian	Null model (3.2)	-	-
	PCA_{Effort} (1)	$PC1_{Effort}$		-	- 0.032 ± 0.071	0.656
	PCA_{DoL} (6)	$PC1_{DoL}$, Material by ♀		Null model (3.4)	-	-
	Synchrony (1)	Together in box		-	- 0.018 ± 0.008	**0.019**
Volume of 3rd egg	PCA_{All} (5)	$PC1_{All}$, $PC2_{All}$	LMM: Gaussian	Null model (9.8)	-	-
	PCA_{Effort} (1)	$PC1_{Effort}$		-	- 0.063 ± 0.087	0.469
	PCA_{DoL} (6)	$PC1_{DoL}$, Material by ♀		Null model (8.5)	-	-
	Synchrony (1)	Together in box		-	- 0.026 ± 0.010	**0.007**

747 ### iv. Behaviour and fitness proxies: Repeatability

748 **Table A 8 |** Repeatability estimates for different behaviours of 16 pairs that were measured repeatedly. State
749 events (SE) were Box-Cox transformed to approximate assumptions for Gaussian data.

Behaviour	Repeatability	SE	2.5 % CI	97.5 % CI	*P*
In box (cumulative) (SE)	0	0.152	0	0.490	1
In box (both birds) (SE)	0	0.155	0	0.518	1
Vigilance (SE)	0	0.154	0	0.509	1
Nest build (SE)	0.094	0.176	0	0.581	0.378
Material	0	0.131	0	0.437	1
Material out	0.031	0.181	0	0.639	0.389
Form cup (SE)	0	0.146	0	0.475	1
Chatter (SE)	0	0.152	0	0.494	0.5
Calls	0	0.103	0	0.357	1
Food sharing	Not converged	-	-	-	-

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751 **Table A 9 |** Repeatability estimates for different correlates of reproductive success.

Fitness measure	Repeatability	SE	2.5 % CI	97.5 % CI	*P*
Clutch size	0	0.078	0	0.278	1
Relative lay date	0.643	0.202	0.025	0.826	**0.023**
Volume first egg	0.598	0.184	0.130	0.843	**0.008**
Volume third egg	0.531	0.193	0.045	0.808	**0.019**

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