Personality shapes pair bonding in a wild bird social system

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Mated pair bonds are integral to many animal societies, yet how individual variation in behaviour influences their formation remains largely unknown. In a population of wild great tits (Parus major), we show that personality shapes pair bonding: proactive males formed stronger pre-breeding pair bonds by meeting their future partners sooner and increasing their relationship strength at a faster rate. As a result, proactive males sampled fewer potential mates. Thus, personality may have important implications for social relationship dynamics and emergent social structure.

Pair bonding—the formation of social relationships between mating partners—has evolved across diverse lineages ranging from simple invertebrate social systems to highly complex human societies6–10. Pair bonds vary in form across the animal kingdom, from relatively ephemeral associations to lifelong monogamous bonds, and shape various ecological processes, such as sexual selection, kinship and social structure, and gene flow11–13. Individuals may depend either partly (for example, humans) or wholly (for example, truly monogamous bird species) on forming these bonds for reproduction, not only for initial matings, but for a diverse range of activities related to subsequent fitness, such as securing breeding locations or providing resources to produce or raise offspring14–16.

While social relationships such as pair bonds are a dyadic property, inevitably, the evolution of the formation of such relationships arises through individual-level processes. Recent research into the genetic and neurobiological proximate mechanisms and ecological consequences of pair bonds has generated widespread and renewed interest in this topic12–15. Yet, how individual-level behavioural variation drives the formation and development of these dyadic relationships remains largely unknown.

Birds provide a model system for investigating pair-bond formation as ~90% of avian species form socially monogamous mated pairs16, and variation in the duration of the pair bond appears to be related to reproductive output in various species17–19. Birds have also been central in advancing the understanding of repeatable individual behavioural differences (termed ‘animal personality’) in natural populations16–18. In many species, variation in individuals’ personalities along measures of the ‘reactive to proactive’ spectrum is known to be consistent across time and contexts, heritable, related to fitness and linked to various ecologically relevant behaviours, including social interactions17,19–21. Nevertheless, the link between personality and pair-bond dynamics in wild animals remains entirely unexplored. This is probably due to the difficulty of quantifying pair-bond formation (which can often take place over prolonged periods before reproduction22–24) among individuals with known personalities, and simultaneously monitoring the social system to enable separation of an individual’s affiliation to their future partner from their general patterns of social activity.

Here, we examine how individual behavioural characteristics shape pair-bonding dynamics by monitoring social associations occurring during the pre-mating winter period (December to March), over three consecutive years, between wild foraging great tits (Parus major) of known personality (quantified on a continuous scale using an activity-exploration assay25,26; see Methods). Importantly, deriving the social network among all dyads each year (winter 2011–2012 = 1,085 individuals; 2012–2013 = 720; 2013–2014 = 805; Supplementary Table 1) enabled us to quantify social associations between individuals and their future breeding partner in relation to their associations with all other birds. In doing so, we could quantify their relative pair-bond strength given their sociability in terms of their propensity to associate with others in general (Fig. 1a).

Considering instances of birds with known personalities in new breeding pairs, for which data on both members were recorded in the previous winter social network (n = 122; 62 males and 60 females), males that were scored as more proactive held stronger relative social affiliation to their future breeding partners over winter than more reactive males (linear mixed model (LMM) with network randomization procedure controlling for network structure and non-independence: estimate = 0.250 ± 0.105, t = 2.373, P = 0.021, Prand = 0.040; see Methods and Supplementary Information for full model and randomization details). However, females’ personality was unrelated to their relative pair-bond strength (Fig. 1b and Supplementary Fig. 2).

Due to large-scale spatiotemporal monitoring of the pre-breeding social associations, it was possible to examine the mechanisms underlying proactive males’ stronger relative affiliations to their future partners. We found no evidence that either sex’s personality was related to the spatial activity overlap in a pair’s winter range (see Supplementary Information). However, more proactive males initially met their future partners sooner as they were observed in the same flock as their partner earlier in the winter than more reactive males (Fig. 1c; generalized LMM (GLMM): estimate = −0.368 ± 0.177, z = −2.076, P = 0.038; also see Supplementary Fig. 3).

Dynamic social networks, created separately for each sampling period (that is, each weekend) throughout each winter, showed that proactive males increased their relative affiliation to their future partner at a faster rate than reactive males (Fig. 2a and Supplementary Fig. 5a). Week-by-week pair-bond strength was significantly predicted by the interaction between the male’s personality and the number of weeks since a partner was first observed. This interaction was strongly positive for proactive males (linear mixed model (LMM) controlling for network structure and non-independence: estimate = 0.707 ± 0.220, t = 3.204, P = 0.001) but not for reactive males (Fig. 2b and Supplementary Fig. 5b). This interaction reflects a phenomenon that we call ‘accelerated pair-bond strength’ occurring in proactive males and implying that proactive males are increasing their pair-bond strength at a faster rate than reactive males, probably due to the increased association with their partner. Accelerated pair-bond strength between individuals with strong positive affiliations may result from proactive males spending more time with their partner and so forming stronger pair bonds, and is a mechanism that could explain the faster rate of pair-bond formation observed among proactive males in our study.

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**Fig. 1 | Relationship between individual personality and dyadic pair bonding.**

**a.** Illustrative social network showing the occurrence of pre-mating pair bonds in the winter social network. Each node shows an individual bird recorded in the winter 2011–2012 network that subsequently bred (in spring 2012) with an individual also recorded in the network. Coloured nodes show those with known personality scores (males, blue; females, green) and the size and shade of the node indicate their position on the reactive–proactive axis (small/light, reactive; large/dark, proactive). Grey nodes represent unknown personality. The thickness of the connecting lines between the nodes shows the strength of the social affiliation between dyads, and affiliations between dyads that subsequently bred together (pair bonds) are curved and coloured red. See Supplementary Fig. 1 for additional network illustration formats.

**b.** Relationship between an individual’s personality score (reactive to proactive; x axis) and the relative affiliation to their subsequent partner (that is, their social association strength with their mating partner relative to the sum of all their associations; y axis). Lines show the LMM fit (see Methods and Supplementary Table 2 for full model details) and the shaded area denotes s.e. (males, blue; females, green). Supplementary Fig. 2 considers additional measures of dyadic pair bonding. **c.** Relationship between personality score and the week when individuals were first observed with their subsequent breeding partner (0 = first observation week of the winter). Lines show the GLMM fit (see Methods and Supplementary Table 3 for full model details) and shaded areas denote s.e. (males, blue; females, green). Supplementary Fig. 3 considers additional measures of the time of subsequent breeding partners’ first meeting.

personality and the time since they first met their future partner (LMM: estimate = 0.026 ± 0.009, t = 2.688, P = 0.007, P rand = 0.008). While females generally showed an increase in their relative pair-bond strength with increased time since first meeting their partner, this was not related to their personality (Supplementary Figs 4a and 5b). Interestingly, the lack of any significant relationship between female personality and all aspects of pre-breeding pair bonding is in line with previous findings showing that male personality is related to various social behaviours and mating behaviours that female personality is unrelated to.11,26,31 This may suggest a general role of male personality in influencing social interactions across various contexts within this population, which could occur through males’ personality directly shaping their own social behaviour, or alternatively through affecting how others choose to interact with them. Further research into the extent and mechanisms driving sex differences in the role that personality plays within this and other systems is now needed.

In addition to showing that more proactive males form stronger pair bonds during the pre-breeding period, both by meeting their future partners sooner and increasing their relationship strength at a faster rate, we also examined the further social consequences of this phenomenon. A strong pair bond may potentially provide various future benefits for an individual, such as ensuring they have a mating partner, potentially allowing earlier breeding or improving offspring rearing, yet efforts to establish and maintain relationships within any social system are likely to also hold some immediate costs.11,31 As such, we found that more reactive (that is, less proactive) males significantly increased the number of females encountered each week throughout the winter compared with more proactive males (GLMM with network randomization: estimate = −0.006 ± 0.002, z = −2.588, P = 0.010, P rand = 0.024; Fig. 2b and Supplementary Fig. 6a). Therefore, early partner choice and maintenance of a tighter pair bond reduced the pool of potential mates sampled. Indeed, it is expected that prioritizing forming a relationship with a particular partner will be traded off against associating with other potential partners in any system where constraints on social associations exist. In this case, if more proactive males ultimately mate with ‘suboptimal’ partners due to reduced sampling, this may provide a novel explanation as to why more proactive males are subsequently more promiscuous during breeding within this population. These differing social costs (that is, less mate sampling) and benefits (that is, stronger pair bonding) of proactive males compared with reactive males help explain how individual-level behavioural variations in personality and pair-bond strength are maintained within populations.

Given these findings, future work should investigate the precise mechanisms underlying how individual-level behavioural variation shapes social relationships across the animal kingdom.12,21,34 This could be considered in terms of how simple individual differences may manifest as complex social behavioural patterns, as well as how these are shaped by genetic or neurobiological factors (both of which are known to contribute to personality and pair bonding).11,30 Furthermore, given that particular individual behavioural types...
may be more likely to produce strong dyadic bonds, the potential effect of population composition (in terms of personality) on the overall architecture of the social system (that is, the density of strong dyadic pair bonds) is of interest, especially given the consequences of network structure for the functioning of almost all social processes, such as the spread of information and disease or the occurrence of cooperation\(^{21,24,25}\).

### Methods

#### Study system.
Wytham Woods, Oxford, United Kingdom (51°46′ N, 1°20′ W) is home to a long-term study population of great tits. The birds form socially monogamous pairs that mostly (>98%) only make one breeding attempt each year, which almost exclusively takes place in nest boxes. Egg laying occurs from April onwards and territory prospecting begins 4–6 weeks before this\(^{1,26}\). Successfully provisioning the chicks after hatching requires both parents, and only a small proportion of young (12–13%) are raised by a different father than the provisioning male due to extra-pair matings\(^{26,39}\). Since 2007, we have also attached unique radio-frequency identification (RFID) microchips to all captured great tits. The RFID tags allow automated recording of the times and locations of individuals’ occurrence at sunflower feeding stations (which are equipped with RFID antennae) as the birds forage in loose aggregations (‘fission–fusion flocks’\(^{46}\)) over the winter. A stratified grid of the RFID feeding stations was deployed throughout the woodland covering 65 fixed locations at ~250 m intervals through winters beginning in 2011, 2012 and 2013. These feeders automatically opened each weekend (that is, Saturday and Sunday; 13 weekends each year from December to March) and scanned for RFID-tagged individuals 16 times per second from pre-dawn until post-dusk.

#### Social networks.
The spatiotemporal data stream of individual RFID detections consists of bursts of activity (as flocks arrive to feed) interspersed with periods of low activity. A machine learning algorithm was used as a robust method to assign each individual record to the flocking event it most likely belonged to\(^{30,40}\). Weighted social networks were then constructed through applying a simple ratio index to the ‘flocking event-by-individual’ matrix\(^{44,46}\) for each year, and also for each separate weekend (Supplementary Methods II). The social associations derived in this way are known to be meaningful and non-random, and carry-over to other social contexts and processes within this population\(^{24,28,32,42}\).

#### Personality assays.
Using standard protocols for this species\(^{41}\), the Wytham population has undergone personality assays since 2005\(^{43,44,47}\). Wild great tits are taken into separate captive housing and individually assessed for their personality the following morning. The personality score is calculated using a standardized methodology based on each bird’s exploration and activity\(^{48}\) while alone in an artificial novel environment. The time of year and number of observations of each bird are also accounted for (see Supplementary Methods III for details). Higher personality scores indicate higher levels of activity and exploration, and these birds are classed as ‘faster explorers’, ‘bolder’ or more ‘proactive’. Individual personality (scored in this way) is known to be repeatable, heritable, and biologically and ecologically relevant\(^{44,45,49}\).

#### Statistical analysis.

**Personality and pair-bond strength.** We first assessed how each individual’s personality predicted the strength of their social network tie to their subsequent breeding partner during the winter pre-breeding period. The primary analysis focused on ‘relative partner affiliation strength’ (or ‘relative pair-bond strength’), which was calculated as the social association strength directed towards their mating partner relative to their weighted degree (that is, the sum of all their associations). This measure ranged from 0 to 1 (where 1 = all their social network associations directed towards their partner). Although this metric was non-symmetric for pairs, it was highly correlated between them, so we considered the sexes separately in all of the models throughout the analysis due to this non-independence, and also in line with previous research and findings that personality can be considered separately between the sexes\(^{44,45}\). Using this individual-based approach, we were able to estimate the relative pair-bond strength of birds of known personality to their partner regardless of whether their partner (or other birds within the system) also had known personalities.

We ran LMMs that included the personality score as a fixed effect, along with age (adult or first year), residency status (Wytham-born or immigrant) and two key winter observational factors: time (that is, weekend) of first observation and number of groups/flocking events they were recorded in\(^{41}\). Furthermore, the random effects of individual and year were included in all models. These factors were consistently controlled for throughout all of the analysis. This primary model here set ‘relative partner affiliation strength’ as the response variable (logit transformed) (Fig. 1b and Supplementary Table 2a). However, we also repeated these models, but replacing ‘relative partner affiliation strength’ with (1) pair simple ratio index (a simple measure of pair-bond strength) and (2) a measure of bond strength relative to any potential intersexual social association differences (Supplementary Methods IV, Supplementary Fig. 2 and Supplementary Table 2b,c).

As network data are non-independent, we also employed a randomization approach to examine the effect of the variable of interest (personality) on pair-bond strength, in line with previous approaches within this system\(^{44,45,47}\). Through randomly swapping the personality of nodes of the same type (in this case, sex) while maintaining the distribution of the data and the relationship of pair-bond strength with the other factors in the model, we generated 10,000 estimates of the coefficients of the relationship expected between personality and pair-bond strength under this null hypothesis. By examining where the observed relationship between personality and pair-bond strength fell within this null distribution, we were able to report the significance of the finding (\(P_{\text{null}}\)) compared with that expected under the same model structures and conditions but when there was no true effect of personality on pair-bond strength (Supplementary Methods IV).

### Table 5

| Personality and temporal patterns in dyadic pair bonding and encounters. |
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| **a** | Three-dimensional surface showing the LMM fit for how the interaction between male personality and weeks since meeting their partner relates to the relative affiliation score (that is, their social association strength with their mating partner relative to the sum of all their associations; see Methods and Supplementary Table 4 for full model details). Males with higher personality scores (more proactive) have a faster rate of increase in their relative affiliation to subsequent breeding partners over increasing time since first meeting them. See Supplementary Fig. 4a for female personality. |
| **b** | Three-dimensional surface showing the GLMM fit for how the interaction between male personality and weeks since the beginning of winter observations relates to the number of females encountered (see Methods and Supplementary Table 5 for full model details). Males with lower personality scores (more reactive) encountered an increasing number of females each week as the breeding season approached. See Supplementary Fig. 4b for female personality. |

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**Fig. 2** | Personality and temporal patterns in dyadic pair bonding and encounters. **a**, Three-dimensional surface showing the LMM fit for how the interaction between male personality and weeks since meeting their partner relates to the relative affiliation score (that is, their social association strength with their mating partner relative to the sum of all their associations; see Methods and Supplementary Table 4 for full model details). Males with higher personality scores (more proactive) have a faster rate of increase in their relative affiliation to subsequent breeding partners over increasing time since first meeting them. See Supplementary Fig. 4a for female personality. **b**, Three-dimensional surface showing the GLMM fit for how the interaction between male personality and weeks since the beginning of winter observations relates to the number of females encountered (see Methods and Supplementary Table 5 for full model details). Males with lower personality scores (more reactive) encountered an increasing number of females each week as the breeding season approached. See Supplementary Fig. 4b for female personality.
Temporal changes in associations. We aimed to examine how individual personality related to temporal changes in social associations, and other individuals as the breeding season drew closer. We created separate, dynamic social networks for each sampling period throughout the pre-mating period and calculated the relative affiliation strength to their future partner at each period (Supplementary Methods III and IV). We used these values as the response variable in a linear mixed model (LMM), which—consistent with the previous models—included the usual fixed effects of age, residency and number of groups they were observed in (that weekend), but also included an interaction between individual personality and ‘weeks since first meeting their partner’. Importantly, this allowed us to examine how the rate of increase in pair-bond strength depended on individual personality (Fig. 2a, Supplementary Fig. 4a and Supplementary Table 4a). We also carried out supplementary analyses (Supplementary Methods VI) along with the usual random and fixed factors as well as the week number (Supplementary Methods III and IV). We used these values as the response variable in a negative binomial GLMM (Supplementary Methods VI) along with the usual random fixed factors as well as the week number (Supplementary Methods III and IV). We also carried out supplementary analyses (Supplementary Methods VI) to ensure that any patterns were not driven by differences in general changes in, and not flocking event together. We used this measure as the response variable in a zero-inflated negative binomial GLMM (Supplementary Methods V). Again, this model was also consistent with the primary LMM as it included the same random effects and fixed effects (individual characteristic and observational terms) and again considered the sexes separately (Fig. 1c and Supplementary Table 3a). We also carried out supplementary analyses (Supplementary Methods V) to verify the results when (1) controlling for any differences in individual gregariousness (Supplementary Fig. 3a and Supplementary Table 3b) and (2) simply considering whether or not the pair was first observed together in their first observational period (Supplementary Fig. 3bc and Supplementary Table 3c).

Ethics. All work (mist netting, ringing and captivity) was carried out under British Trust for Ornithology (A5435) and Natural England licences (20131205 and 20123075), and adhered to UK standard requirements.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability All data supporting the findings of this study are available within the paper and its Supplementary Information files.

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References
1. Wittenberger, J. F. & Tilson, R. L. Annu. Rev. Ecol. Syst. 11, 197–232 (1980).
2. Reichard, U. H. & Boesch, C. (eds) Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals (Cambridge Univ. Press, Cambridge, 2003).
3. Emlen, S. T. & Oring, L. W. Science 197, 215–223 (1977).
4. Lukas, D. & Clutton-Brock, T. H. Science 341, 526–530 (2013).
5. Song, Z. & Feldman, M. W. J. Evol. Biol. 26, 963–970 (2013).
6. Kageyama, D. G. Q. Rev. Biol. 52, 39–68 (1977).
7. Black, J. M. Partnerships in Birds: The Study of Monogamy (Oxford Univ. Press, Oxford, 1996).
8. Amadei, E. A. et al. Nature 546, 297–301 (2017).
9. Young, I. J. & Wang, Z. X. Nat. Neurosci. 7, 1048–1054 (2004).
10. Lim, M. M. et al. Nature 429, 754–757 (2004).
11. Firth, J. A. et al. Curr. Biol. 25, 3138–3143 (2015).
12. Lack, D. Ecological Adaptations for Breeding in Birds (Chapman and Hall, London, 1968).
13. Perrins, C. M. & MceIlreavy, R. H. Ibis 127, 306–315 (1983).
14. Sanchez-Macouzet, O. et al. Proc. Roy. Soc. B 281, 20132843 (2014).
15. Fayet, J. L. et al. Mar. Ecol. Prog. Ser. 569, 243–252 (2017).
16. Reale, D. et al. Biol. Rev. 82, 291–318 (2007).
17. Bengston, S. E. et al. Nature Ecol. Evol. 2, 944–955 (2018).
18. Dingemanse, N. J. et al. Anim. Behav. 64, 929–938 (2002).
19. Sih, A. et al. Trends Ecol. Evol. 19, 372–378 (2004).
20. Apolin, L. M. et al. Ecol. Lett. 16, 1365–1372 (2013).
21. Krause, J. et al. Philos. Trans. R. Soc. B 365, 4099–4110 (2016).
22. Quinn, J. L. et al. Anim. Ecol. 78, 1203–1215 (2009).
23. Quinn, J. L. et al. Proc. Roy. Soc. B 279, 1919–1926 (2012).
24. Sih, A. et al. Ecol. Lett. 15, 278–289 (2012).
25. Dingemanse, N. J. et al. Proc. Roy. Soc. B 271, 847–852 (2004).
26. Patrick, S. C. et al. Proc. Roy. Soc. B 279, 1724–1730 (2012).
27. Quinn, J. L. et al. Anim. Ecol. 80, 918–928 (2011).
28. Smith, B. R. & Blumstein, D. T. Behav. Ecol. 19, 448–455 (2008).
29. Favati, A. et al. Proc. Roy. Soc. B 281, 20132531 (2014).
30. Teitelbaum, C. S. et al. Anim. Behav. 134, 147–154 (2017).
31. Johnson, K. V. A. et al. Anim. Behav. 128, 21–32 (2017).
32. Gunnarsson, T. G. et al. Nature 431, 646 (2004).
33. Griffith, S. C. et al. Proc. Roy. Soc. B 278, 2798–2805 (2011).
34. Firth, J. A. et al. Proc. Roy. Soc. B 284, 20171939 (2017).
35. Apolin, L. M. et al. Nature 518, 538–541 (2015).
36. Allen, B. et al. Nature 544, 227–230 (2017).
37. Firth, J. A. & Sheldon, B. C. Proc. Roy. Soc. B 282, 20142350 (2015).
38. Firth, J. A., Verhulst, B. L., Crates, R. A., Garroway, C. J. & Sheldon, B. C. J. Avian Biol. https://doi.org/10.1111/jav.01740 (2018).
39. Firth, J. A. et al. Evolution 69, 1336–1344 (2015).
40. Farine, D. R. et al. R. Soc. Open Sci. 2, 150057 (2015).
41. Firth, J. A. & Sheldon, B. C. Ecol. Lett. 19, 1324–1332 (2016).
42. Psorakis, I. et al. Behav. Ecol. Sociobiol. 69, 857–866 (2015).
43. Apolin, L. M. et al. Anim. Behav. 108, 117–127 (2015).
44. Firth, J. A. et al. Biol. Lett. 12, 20160144 (2016).
45. Firth, J. A. et al. Proc. Roy. Soc. B 284, 20170299 (2017).
46. Verbeek, M. E. M. et al. Anim. Behav. 48, 1113–1121 (1994).

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Author contributions J.A.F. conceived the study, carried out the analysis and wrote the first draft. J.A.F., E.F.C., C.C.I., J.L.Q. and B.C.S. interpreted the data and planned the draft. J.A.F., E.F.C., L.M.A., A.C. and K.M. collected the data. All authors contributed significantly to revising the manuscript.

Competing interests The authors declare no competing interests.

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Software and code

Policy information about availability of computer code

Data collection
Automated detection of RFID records was carried out by Trovan RFID readers, Dorset ID, Aalten, Netherlands. Recording of animal personality was carried out using the Handheld Psion Workabout, Noldus Information Technology, Nottingham, UK (Quinn et al. 2009, 2011; J. Anim. Ecol).

Data analysis
Data analysis was carried out in Matlab and R 3.3.2 under standard previously described protocols. No unreported custom software was used.

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Life sciences study design

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- **Sample size**
  No a priori sample size calculation was performed due to the complexity of the system. Full sample size information is reported in Supplementary Table 1. The raw data consisted of 8.1 million RFID records from 1833 individual wild great tits (Parus major). Previous research within this study system has suggested that this sample size is sufficient for reliably inferring social networks (e.g. Aplin et al. 2015 An Behav; Firth & Sheldon 2016 Ecol Lett)

- **Data exclusions**
  No data was excluded from the analysis. Limits on which subsets of the data could be used to each analysis is provided in Supplementary Table 1.

- **Replication**
  The study was carried out within a population containing 1833 RFID tagged great tits (Parus major) over three years (Dec 2011-Mar 2012, Dec 2012-Mar 2013, Dec 2013-Mar 2014)

- **Randomization**
  As no experiments took place, sampled individuals were not allocated to experimental groups. All potentially confounding variables are reported in full and network randomizations were used within the analysis.

- **Blinding**
  RFID detection data was collected automatically from RFID data loggers (blind to researcher). All personality scoring was carried out under a standardised protocol and the data collector had no knowledge of individuals’ pair bonding dynamics (i.e. blind to the variable of interest).

Reporting for specific materials, systems and methods

| Materials & experimental systems | Methods |
|---------------------------------|---------|
| n/a                             | n/a     |
| Unique biological materials     | Involved in the study     |
| Antibodies                      |         |
| Eukaryotic cell lines           |         |
| Palaeontology                   |         |
| Animals and other organisms     |         |
| Human research participants     |         |

| Methods                         |
|---------------------------------|
| Involved in the study           |
|                                 |
| ChIP-seq                        |
| Flow cytometry                  |
| MRI-based neuroimaging          |

Animals and other organisms

Policy information about studies involving animals. ARRIVE guidelines recommended for reporting animal research

- **Laboratory animals**
  The study did not involve laboratory animals

- **Wild animals**
  All work (mist netting, ringing and captivity) of the great tits (Parus major) within this study was carried out under BTO (AS435) and Natural England licences (20131205 and 20123075), and adhered to UK standard requirements and protocols.
Personality-assayed birds were transported to John Krebs Field Station (Oxford University) within 1.5 h of capture, and monitored throughout the first day. They were housed at an ambient temperate indoors and under a natural light regime. Birds were kept in separate wire-mesh cages (45 x45 x68 cm) which neighboured one another but did not allow physical contact. All cages were equipped with roost boxes, and birds were provided with food (live mealworms and seed mix) and water on a daily basis. All individuals were weighed before being release at the site they were captured and changes in all individuals’ body mass during their period of captivity were all within the natural fluctuation range.