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Authors	Firth, Josh A.;Cole, Ella F.;Ioannou, Christos C.;Quinn, John L.;Aplin, Lucy M.;Culina, Antica;McMahon, Keith;Sheldon, Ben C.
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Personality shapes pair bonding in a wild bird social system

Josh A. Firth[1,2,*], **Ella F. Cole**[1], **Christos C. Ioannou**[3], **John L. Quinn**[4], **Lucy M. Aplin**[1,5], **Antica Culina**[1,6], **Keith McMahon**[1], and **Ben C. Sheldon**[1]

[1]Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK [2]Merton College, Merton Street, University of Oxford, Oxford, OX1 4JD [3]School of Biological Sciences, University of Bristol, Bristol, BS81TQ [4]School of Biological, Earth and Environmental Sciences, University College Cork, North Mall, Cork, Ireland [5]Max Planck Institute for Ornithology, Radolfzell, Germany [6]Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, Netherlands

Abstract

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 and, as a result, 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 societies1,2. Pair bonds vary in form across the animal kingdom, from relatively ephemeral associations to life-long monogamous bonds, and shape various ecological processes, such as sexual selection, kinship and social structure, and gene flow2–5. Individuals may depend either partly (e.g. humans) or wholly (e.g. 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 offspring2,6,7.

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[*]Correspondence: Dr. Josh A. Firth joshua.firth@zoo.ox.ac.uk.

Data Availability
All data supporting the findings of this study are available with the paper (see supplementary information files)

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

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. & B.C.S. interpreted the data and planned the draft, J.A.F., E.F.C., L.M.A., A.C., & 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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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 topic8–11. 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 pairs7,12, and variation in the duration of the pair-bond appears to be related to reproductive output in various species13–15. 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 interactions17,19–29. Nevertheless, the link between personality and pair-bond dynamics in wild animals remains entirely unexplored. This is likely due to the difficulty of quantifying pair-bond formation (which can often take place over prolonged periods before reproduction7,30) amongst individuals with known personalities, and simultaneous 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 assay16,22 - see Methods). Importantly, deriving the social network amongst all dyads each year (winter 2011/12=1085 individuals, 2012/13=720, 2013/14=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. By 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, of which both members were recorded in the prior winter social network (n=122, 62 males, 60 females), males 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, p_{rand}=0.040, see Methods and Supplementary Information for full model and randomization details throughout). Females' personality, however, was unrelated to their relative pair-bond strength (Fig. 1b; Supplementary Figure 2).

Due to the 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

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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 Linear Mixed Model: Estimate=-0.368±0.177, z=-2.076, p=0.038; Also see Supplementary Figure 3).

Dynamic social networks, created separately for each sampling period (i.e. each weekend) throughout each winter, showed that proactive males increased their relative affiliation to their future partner at a faster rate than reactive males did (Fig 2a; Supplementary Figure 5a). Week-by-week pair-bond strength was significantly predicted by the interaction between the male's 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 again was not related to their personality (Supplementary Figures 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 to20,26,31. 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 examine 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 rearing2,7,13,30,32, yet efforts to establish and maintain relationships within any social system are likely to also hold some immediate costs11,33. As such, we found that more reactive (i.e. less proactive) males significantly increased the number of females encountered each week throughout the winter in comparison to more proactive males (GLMM with network randomization: Estimate=-0.006±0.002, z=-2.588, p=0.010, p_{rand} 0.024 - Fig. 2b; Supplementary Figure 6a). Therefore, early partner choice and maintenance of a tighter pair bond reduced the pool of potential mates sampled. Indeed, it is expected that prioritising 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 'sub-optimal' 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 population26. These differing social costs (i.e. less mate sampling) and benefits (i.e. stronger pair-bonding) of proactive males in comparison to reactive males help explain how individual-level behavioural variation in personality, and pair-bond strength, are maintained within populations.

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Given these findings, future work should investigate the precise mechanisms underlying how individual-level behavioural variation shapes social relationships across the animal kingdom5,20,21,34. This could be considered in terms of how simple individual differences may manifest as complex social behavioural patterns34 as well as how this is shaped by genetic or neurobiological factors (both of which are known to contribute to personality and pair-bonding)8,10. 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 (i.e. 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 cooperation5,11,21,35,36.

Methods

Study System

Wytham Woods, Oxford, UK (51°46'N, 1°20'W) is home to a long-term study population of great tits. The birds form socially monogamous pairs which mostly (>98%) only make one breeding attempt each year that almost exclusively takes place in nestboxes. Egg laying occurs from April onwards and territory prospecting begins 4-6 weeks prior to this13,37,38. Successfully provisioning the chicks after hatching requires both parents, and only a small proportion of young (12-13%) are sired by a different father than the provisioning male due to extra-pair matings26,39. Since 2007, we have also attached unique RFID-microchips to all captured great tits. The RFID-tags allow the 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' flocks40,41) over the winter. A stratified grid of the RFID feeding stations was deployed throughout the woodland covering 65 fixed locations at ~250m intervals through winters beginning 2011, 2012 and 2013. These feeders automatically opened each weekend - 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 spatio-temporal datastream of individual RFID detections consists of bursts of activity (as flocks arrive to feed) interspersed by 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 to42. Weighted social networks were then constructed through applying the Simple Ratio Index (SRI) to the 'flocking event-by-individual' matrix37,40–45 for each year, and also for each separate weekend (Supplementary Methods II). The social associations derived in this way are known to be meaningful, non-random and carry-over to other social contexts and processes within this population11,20,35,37,40–45.

Personality Assays

Using standard protocols for this species46, the Wytham population has undergone personality assays since 200520,22,23,26,27. Wild great tits are taken into separate captive housing and individually assayed for their personality the following morning. The

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personality score is calculated using a standardized methodology based on each bird's exploration and activity16 whilst alone in an artificial novel environment. The time of year and number of observations of each bird is also accounted for (see Supplementary Methods III for details). Higher personality scores indicate higher levels activity and exploration, and these birds are classed as 'faster explorers', 'bolder' or more 'proactive' and individual personality (scored in this way) is known to be repeatable, heritable, and biologically and ecologically relevant18,20,22,23,26,27,31,46.

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, i.e. 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 sexes20,26,31. Using this individual-based approach, we were able to estimate the relative pair-bond strength to 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 which 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 (i.e. weekend) of first observation and number of groups/flocking events they were recorded in43. Further, the random effects of individual and year ID were included in all models. These factors were consistently controlled for throughout all the analysis. This primary model here set 'relative partner affiliation strength' as the response variable (logit transformed) (Figure 1b; Supplementary Table 2a). However, we also repeated these models but replacing 'relative partner affiliation strength' with (a) pair SRI (a simple measure of pair bond strength) and (b) a measure of bond strength relative to any potential intersexual social association differences (Supplementary Methods IV; Supplementary Figure 2; Supplementary Table 2b & 2c).

As network data is 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 system11,31,37,40,41,43,45. Through randomly swapping the personality of nodes of the same type (in this case, sex) whilst maintaining the distribution of the data and the relationship of pair bond strength with the other factors in the model, we generated 10000 estimates of the coefficients of the relationship expected between personality and pair-bond 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_{rand}) in comparison to

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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).

Spatial overlap and time of meeting—To dissect how individual differences in yearly pre-mating pair strength may arise, we considered spatial and temporal differences in bond formation. Firstly, we examined the extent to which individuals' shared the same spatial range as their future partner. We repeated the same model structure (as above) but set the response variable as individuals' winter spatial range overlap instead of their relative pair-bond strength. Winter spatial overlap41 was based on how both members of the pair distributed their activity in space and ranged from 0 to 1 (0 = never overlapped and 1 = spatial activity patterns fully overlapped – Supplementary Methods V – Supplementary Table 2d).

Secondly, we considered the time at which a bird first meets its future partner. We defined first meeting as the numerical count of the first sampling period (weekend) in which a pair was first observed in the same 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 (Figure 1c; Supplementary Table 3a). We also carried out supplementary analysis (Supplementary Methods V) to verify the results when (a) controlling for any differences in individual gregariousness (Supplementary Figure 3a; Supplementary Table 3b) and when (b) simply considering whether or not the pair was first observed together in their first observational period (Supplementary Figure 3b & 3c; Supplementary Table 3c).

Temporal changes in associations—We aimed to examine how individual personality related to temporal changes in social associations with their future partner and other individuals as the breeding season drew closer. We created separate, dynamic, social networks for each sampling period throughout the pre-mating period41,43,45 and calculated the relative affiliation strength to their future partner at each period (Supplementary Methods III & IV). We used these values as the response variable in an 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 (Figure 2a; Supplementary Figure 4a; Supplementary Table 4a). We also carried out supplementary analysis (Supplementary Methods VI) to ensure that any patterns were not driven by differences in general changes in intersexual social associations (Supplementary Figure 5; Supplementary Table 4b).

We also used the weekly networks to examine whether the number of individuals of the opposite sex that they encountered changed over the winter and whether this depended on individual personality. We calculated the number of unique individuals of the opposite sex each individual encountered each week (i.e. their weekly intersexual binary degree), and set this numerical count the response variable in a negative binomial GLMM (Supplementary

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Methods VI) along with the usual random and fixed factors as well as the week number (i.e. observation period). Importantly, fitting an interaction between week and personality allowed examination of how intersexual encounters through time depended on individual personality (Figure 2b; Supplementary Figure 4b; Supplementary Table 5a). To ensure that any ascribed changes were not due to general changes in degree (rather than intersexual encounters), we also (a) included weekly intrasexual degree as a fixed effect and (b) re-ran the same model but considering weekly intrasexual encounters as the response variable (Supplementary Methods VI; Supplementary Figure 6; Supplementary Table 5b & 5c).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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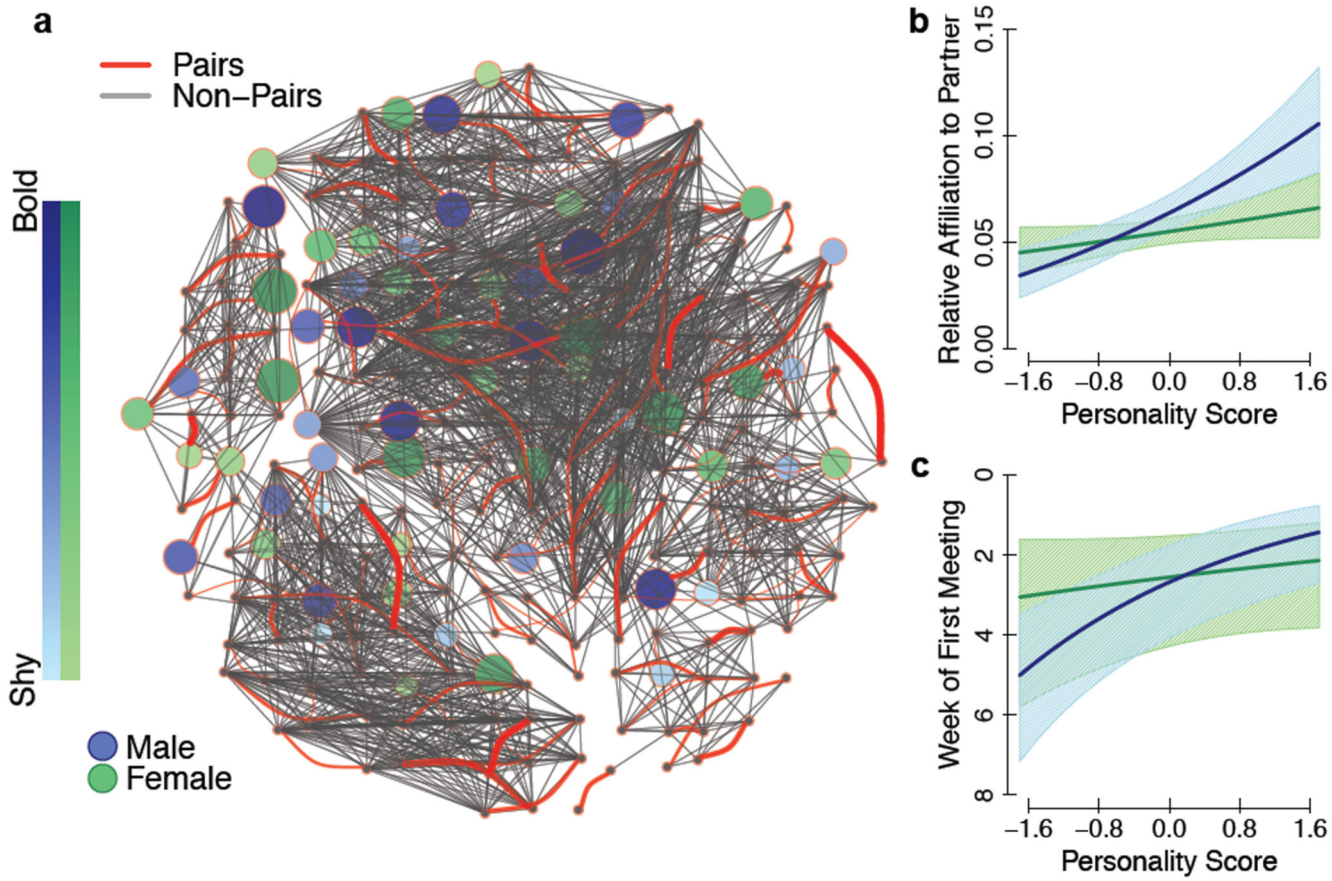


Fig 1. The relationship between individual personality and dyadic pair-bonding.

a: An illustrative social network showing the occurrence of pre-mating pair-bonds and 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 network. Coloured nodes show those with known personality scores (males = blue, females = green) and the size and shade of the node indicates their position on the reactive-proactive axis (small/light = reactive, large/dark = proactive). Grey nodes are those of unknown personality. The thickness of the connecting lines between the nodes show the strength of the social affiliation between dyads, and affiliations between dyads which subsequently bred together (pair-bonds) are curved and coloured red. See Supplementary Figure 1 for additional network illustration formats. **b**, the relationship between an individual's personality score (reactive to proactive – x axis) and the relative affiliation to their subsequent partner (i.e. their social association strength with their mating partner relative to the sum of all their associations - y axis). Lines show LMM fit (see Methods, and Supplementary Table 2 for full model details) with shaded area denoting standard error (males = blue, females = green). Supplementary Figure 2 considers additional measures of dyadic pair-bonding. **c**, personality score and the week that individuals were first observed with their subsequent breeding partner (0= first observation week of the winter). Lines show GLMM fit (see Methods, and see Supplementary Table 3 for full model details) with shaded

area denoting standard error. Supplementary Figure 3 considers additional measures of the time of subsequent breeding partners' first meeting.

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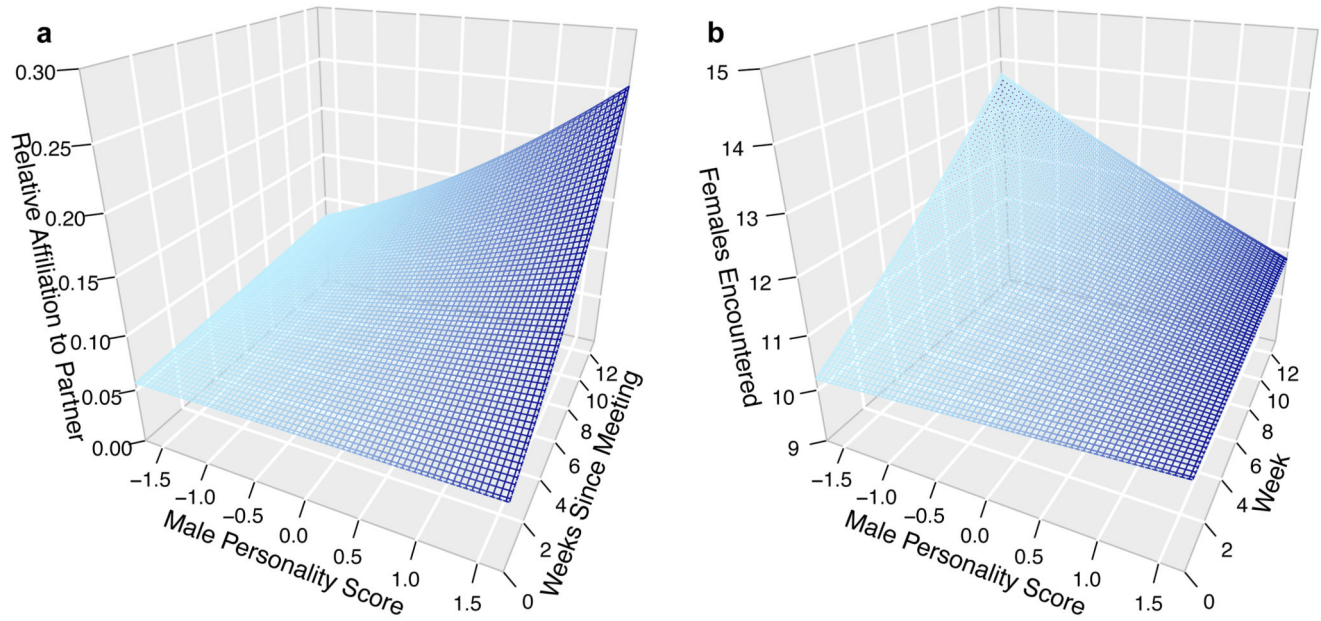


Fig 2. Personality and temporal patterns in dyadic pair-bonding and encounters.

a: 3D surface showing the LMM fit of the interaction between male personality and weeks since meeting their partner on the relative affiliation score i.e. 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 partner over the increasing time since first meeting them. See Supplementary Figure 4a for female personality. **b**, 3D surface showing the GLMM fit of the interaction between male personality and week (since the beginning of winter observations) on 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 approaches. See Supplementary Figure 4b for female personality.

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