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Title

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Abstract

Individual variation in the timing of activities is increasingly being reported for a wide variety of species, often measured as the timing of activity onset in the morning. However so far, the adaptive significance of consistent variation in temporal phenotypes (i.e. the chronotype) remains largely elusive. Potentially, differences in timing of activities may arise as a result of competition among individuals for resources. Less aggressive individuals may try to avoid competition by becoming active earlier during the day when other individuals are still inactive, leading to a positive correlation between chronotype and aggressive personality type (i.e. a behavioural syndrome). To investigate this, we assessed the chronotype of female great tits (*Parus major*) by measuring emergence time from the nest box in the morning and experimentally tested their levels of same-sex aggression through simulated territorial intrusion tests. Contradicting our initial hypothesis, consistently more aggressive females became active earlier during the day compared to less aggressive females, which could be caused by shared underlying mechanisms, like pleiotropic effects of sex hormones or gene pleiotropy, which potentially impose constraints on the independent evolution of both traits. Surprisingly, on the within-individual level we found an opposing correlation between emergence time and aggression. Our findings highlight the need for further investigations into the interplay between chronotype and aggression that take the underlying mechanisms into account in order to understand the adaptive significance of this trait association.

Keywords: Aggression, Behavioural Syndrome, Chronotype, Competition, Personality, Temporal Phenotype

Introduction

In both humans and non-human animals, behaviour and physiology often show rhythmicity that is aligned with the day and night cycle. For example, sleep-wake cycles and body temperature fluctuations follow patterns of approximately 24h (e.g. Aschoff, 1967; Moore, 2007; Refinetti & Menaker, 1992; Strauß et al., 2022). This rhythmicity is maintained by the circadian clock, a biochemical timekeeping system that is sensitive to light. In birds, among individual differences have been observed in the timing of the circadian clock (Helm & Visser, 2010; Lehmann et al., 2012; Tomotani et al., 2023). Such differences become apparent when studying the wake-up time in the morning or the timing of the onset of sleep in the evening. Consistency in the timing of activities is typically referred to as an individual's chronotype. Although an increasing number of studies has demonstrated the existence of chronotypes in multiple species (Alós et al., 2017a; Chmura et al., 2020; Dominoni, 2013; Graham et al., 2017; Grunst et al., 2021; Maury et al., 2020; Meijdam, Müller, & Eens, 2022; Schlicht & Kempenaers, 2020; Steinmeyer et al., 2010; Stuber et al., 2015), its adaptive significance and how this variation is maintained in the population remain largely unknown.

Behavioural traits that consistently vary among individuals across contexts and over time are often considered as personality traits (Réale et al., 2007). The existence of consistent differences among individuals implies that behavioural plasticity is limited and that some individuals may be coping better in certain environments than others (Dingemanse et al., 2012). Natural and sexual selection may thus act upon such personality traits, and in order to evolve they should be genetically underpinned (Dochtermann et al., 2015, 2019). Although daily activity patterns are often highly repeatable across time and context and the circadian period length, a key regulator of the chronotype (Tomotani et al., 2023), is highly heritable ($h^2 = 0.86$, SD = 0.24; Helm & Visser, 2010), only few studies have considered it as a personality trait in non-human animals (Randler, 2014). Furthermore, individual variation in chronotype might come with fitness consequences. For example, starting activity early could improve feeding opportunities, while it might increase predation risk by (nocturnal) predators (Helm et al., 2017). The timing of sexual displays in turn may affect mating success (Hau et al., 2017). Indeed, in male Eastern kingbirds (*Tyrannus tyrannus*) and blue tits (*Cyanistes caeruleus*), individuals that start dawn song earlier in the morning are more likely to gain extra pair paternity (Dolan et al., 2007; Poesel et al., 2006; Schlicht et al., 2023). However, in blue tits experimentally advancing the dawn song did not increase extra pair success in males (Santema & Kempenaers, 2023) and chronotype was not related to extra pair success in females (Schlicht et al., 2014). Chronotype did also not affect the female's reproductive success in blue and great tits (Steinmeyer et al., 2013; Womack, 2020; but see Womack et al., 2023). Thus, the current state of knowledge is still inconclusive, especially in females.

Importantly, selection may act on suites of correlated behaviours simultaneously (Bell, 2006; Sih et al., 2004). Such a correlation between two or more behavioural traits at the among-individual level is typically referred to as a behavioural syndrome (Sih et al., 2004). For chronotypes, behavioural syndromes are as of yet underexplored at least in non-human species (but see Alós et al., 2017; Amin et al., 2016). Behavioural syndromes can arise by multiple processes. One such process is described by the adaptive hypothesis, which states that correlations between behavioural traits emerge when the correlation itself is adaptive (Bell, 2005; Herczeg & Garamszegi, 2012). In other words, the combination of two or more traits is favoured by correlational selection (Bell, 2005). For example, in sticklebacks (*Gasterosteus aculeatus*) some individuals may opt for the safety in numbers by schooling, which does not go well with aggressiveness towards conspecifics (Magurran & Seghers, 1991). Other individuals may inspect a predator to gain information (Bell & Sih, 2007), where aggressiveness may be beneficial, potentially leading to a behavioural syndrome between the antipredator strategy and aggression (see also Huntingford, 1976). However, behavioural syndromes do not need to be adaptive *per se*. From a mechanistic perspective they may also arise when different behaviours are controlled by the same gene(s) (i.e., gene pleiotropy), neurotransmitters or hormones. Such shared underlying drivers of behaviour may constrain the independent evolution of the traits involved, for example through antagonistic selection, so that the trait optima do not coincide. This hypothesis is referred to as the constraint hypothesis (Bell, 2005).

Finally, individual variation may also relate to inter-individual differences in realized ecological niche dimensions (i.e. individual niche specialisation; Bolnick et al., 2003). One of the main drivers of individual specialisation is thought to be intraspecific competition, as it can favour niche width expansion or diversification (Dall et al., 2012; Svanbäck & Bolnick, 2006). Temporal segregation in daily activity patterns within species, which may result from among-individual differences in chronotype, could thus be related to competition (Alanärä et al., 2001; Howerton & Mench, 2014; Stone et al., 2019), and may be related to other personality traits, if they determine the competitive ability of the individual (Gharnit et al., 2020), leading to behavioural syndromes.

Competitive ability is, amongst others, related to aggression (Blanchard et al., 1988; O'Shea et al., 2017), which serves a critical function in resolving conflicts among conspecifics when they compete for resources like territories, partners or food sources (Pandolfi et al., 2021), and can be both defensive or offensive (Blanchard et al., 2003). Conflict resolution can involve signalling, such as through bird song, or physical aggression (van Staaden et al., 2011), with the latter carrying the potential risk of injury. Individuals with low aggression levels could benefit from being active during periods when others are asleep, which enables them to obtain the necessary resources. In contrast, starting activity early may not be necessary to more aggressive individuals. Therefore, we predict a positive correlation between chronotype and aggression. Such a positive relationship between chronotype and aggression has been reported in pearly razor fish (*Xyrichtys novacula;* Martorell-Barceló et al., 2023).

We used female great tits to test these predictions, as previous studies in our population have shown both short- and long-term repeatable variation in aggression (Thys et al., 2021) and emergence time (i.e. the timing of activity onset in the morning; Meijdam, Müller, & Eens, 2022), which is a prerequisite for the existence of behavioural syndromes. Moreover, aggression in great tits is related to exploration and risk taking (Carere et al., 2005; Hollander et al., 2008; Thys et al., 2017), and all three behavioural traits have been related to dominance in foraging contexts and higher foraging flexibility (Bibi et al., 2019; Coomes et al., 2022; Dingemanse & de Goede, 2004; Verbeek et al., 1996), indicating that more aggressive great tits are likely to be better competitors. To test for a behavioural syndrome between chronotype and aggression, we measured emergence time from the nest box in the morning as a proxy for chronotype, and determined aggression by experimentally simulating territorial intrusions, both during the egg laying period of the breeding season. As phenotypic correlations between two (or more) behavioural traits may suggest the presence of a behavioural syndrome, but could also arise from correlated plasticity, we partitioned the phenotypic correlations at two levels: the among-individual level, which corresponds to a potential behavioural syndrome, and the within-individual level, which is indicative of correlated plasticity (Dingemanse et al., 2010).

Material & Methods

Study population

All data were collected in a suburban nest box population of great tits (± 170 nest boxes), in Wilrijk (Antwerp), Belgium (51°09'46.1"N, 4°24'13.3"E) during the breeding season (March – May) of 2018 and 2019 as a part of two previous studies (Meijdam, Müller, & Eens, 2022; Thys et al., 2021). All nest boxes were monitored for nest building, egg laying and incubation. During previous breeding seasons and during roosting in winter individual birds were equipped with unique combinations of rings around their tarsi, enabling individual recognition. Each bird received a metal ring and three colour rings, one of which containing a PIT-tag (passive integrated transponder; internal diameter 2.6 mm, length 8.0 mm, EM4102, 125 KHz, Eccel Technology Ltd, Aylesbury, UK). Age (yearling vs. older) and sex were determined based on plumage characteristics upon capture.

Ethical note

This study was approved by the ethical committee of the University of Antwerp (ID numbers: 2016-87, 2018-50, 2017-23 and 2017-61) and was performed in accordance with Belgian and Flemish laws regarding animal welfare, adhered to the ASAB/ABS guidelines for the use of animals in behavioural research and teaching, and complies with ARRIVE guidelines. The Royal Belgian Institute of Natural Sciences (KBIN) provided ringing licenses for all authors and technicians. Handling time was minimized as much as possible. All other methods described below are non-invasive.

Emergence time

During the breeding season only females sleep inside the nest box. Female emergence times from the nest box were measured as a proxy for activity onset (see Meijdam, Müller, & Eens, 2022; Meijdam, Müller, Thys, et al., 2022) during the egg laying period of the breeding season, since both aggression and emergence time could simultaneously be measured during this period. Emergence times reported here were mainly determined using SongMeters (682 datapoints on 209 females, SongMeterTM SM2+; Wildlife Acoustics, Inc, U.S.), but during the peak of the 2018 breeding season the number of females that had to be measured on the same day was higher than the amount of SongMeters available, so we additionally used radio-frequency identification (RFID) loggers (14 datapoints on 10 females, EM4102 data logger, Eccel Technology Ltd, Aylesbury, U.K.; Iserbyt et al., 2018) and infrared sensitive cameras (1 datapoint on 1 female, Pakatak PAK-MIR5, Essex, UK, (Grunst et al., 2022)). Across the breeding season emergence times were often measured with both RFID loggers and SongMeters simultaneously. On average they differed by 1.5 ± 0.4 min (mean ± standard error; n = 633 mornings recorded at 74 nest boxes, Grunst et al. unpublished). To ascertain no bias in the results due to the different methodologies used, we performed our statistical analyses once with all data included and once with only SongMeter data included. Since results of both analyses gave similar results we only present those of the analysis using all emergence time data.

SongMeters were placed on top of the nest box with one microphone inside and the other microphone outside the nest box. Sound was recorded from 0400 hours to 0800 hours during the winter time period. After the clock changed to summer time sound was recorded from 0300 hours to 0800 hours. Avisoft SASLab Pro 5.2.14 was used to visualize the sound profiles (Figure S1) and emergence time was determined by inspecting the sonogram and audio (Specht, 2002). When a female leaves the nest box in the morning the sound of the body moving through the nest box opening can be heard on the inside microphone, while the wing beats during take-off can be heard on both microphones (Halfwerk et al., 2011). The moment of take-off was used as the emergence time. Due to the order of sounds made by the female, it is easy to identify the direction of the movement. RFID loggers register PIT-tagged individuals when they fly through the two antennas, which were placed around the nest box opening. Both the unique PIT-tag number and the time of leaving/entering the nest box was saved (for more details see Iserbyt et al., 2018). Infrared sensitive cameras were installed under the lid of the nest box, pointing downwards. The cameras recorded immediately after installation at least two hours before sunset and were switched off on collection the next morning at least two hours after sunrise (Raap et al., 2015). Within years each female was measured on 1 to 7 consecutive mornings during the egg laying period.

Aggression

Aggression tests were performed at day 2 and 5 (or day 3 and/or 6 if the female was not present on the first time point) of the egg laying period in both years, with day 1 referring to the day the first egg was laid (Thys et al., 2017). A territorial intrusion was simulated by placing a taxidermic mount of a female great tit inside a cage of mesh wire (decoy; N_{decoy} = 6) on top of the focal female's nest box, following Thys et al. (2017). From the moment the focal female was present within a radius of 15 meters around the nest box, her behaviour was observed ($N_{observer}$ = 6) for 5 minutes from a distance of approximately 15 meters. For the focal female, the following aggression parameters were scored: the minimal distance to the decoy (approach distance, in meters), the number of alarm calls produced, the number of attacks towards the decoy and the time spent on the mesh wire cage (time decoy, in seconds). All tests were performed between 0730 hours and 1200 hours in the morning.

Statistical Analyses

In total, data on emergence time were collected for 207 females. Data of 15 females were removed from the dataset since their age remained unknown due to nest failure before they could be captured. The final dataset contained 43 females for which emergence times were measured in both years and 149 females for which emergence times were measured in one year (average number of measurements within years = 3.71, SD = 0.98). For 181 females we also obtained data on aggression (N_{test} = 401), with 39 females measured in both years and 142 females measured in one year (average number of measurements within years = 1.72, SD = 0.45). All statistical analyses were performed in R 4.1.3 (R Core Team, 2013). The MCMCglmm package (version 2.35) was used throughout to fit multivariate mixed models (Hadfield, 2010). Response variables were scaled to unit variance prior to all analyses.

We performed two consecutive analyses. First, we explored the among- and within-individual (co)variation between the different aggression parameters observed during territorial intrusion. To this end, we constructed a multivariate mixed model (Araya-Ajoy & Dingemanse, 2014; Dingemanse & Dochtermann, 2013; Houslay & Wilson, 2017) which included the approach distance (multiplied by -1), the number of calls, the number of attacks and the time on the decoy as response variables of which the latter three were square root transformed. Based on previous findings (Thys et al., 2021), year (2018 vs. 2019) and age (yearling vs. older) were included as fixed effects. Female identity (N = 181) was included as random effect, which enabled us to partition behavioural (co)variation into its among-and within-individual components (Dingemanse & Dochtermann, 2013). We did not include decoy or observer identity as random effects since our previous work has shown they are of no or minor importance in explaining variation in aggression parameters (see Thys et al., 2020; Thys et al., 2021). From this model, the repeatability of each separate aggression parameter was calculated as the among-individual variance divided by the total phenotypic variance (i.e. the sum of among- and within-individual variance; Nakagawa & Schielzeth, 2010). Among- and within-individual covariances between the different aggression parameters were converted into correlations by dividing the respective covariance by the square root of the product of the respective variances, thereby allowing easier interpretation.

Second, a multivariate mixed model was constructed to investigate the among- and within-individual (co)variation between emergence time from the nest box and aggression. Results of our first multivariate mixed model revealed that time on the decoy during territorial intrusion covaried with the number of attacks on both the among- and within-individual level (see Results and Table 1) so we opted to use time on the decoy in further analyses as an operational measure of aggression (see also Araya-Ajoy & Dingemanse, 2014). Hence, we constructed a bivariate mixed model with time on the decoy (square root transformed) and emergence time from the nest box as response variables. As we had more measurements for emergence time than for time on decoy, the measurements were not always matched. For both traits, we included year (2018 vs. 2019), age (yearling vs. older) and a polynomial date (mean-centred within years) effect up to the second order as fixed effects (Meijdam, Müller, & Eens, 2022; Thys et al., 2021). For emergence time, we also included the temperature (T°) at sunrise (mean-centred within years; Schlicht & Kempenaers, 2020). Female identity (N = 181) was included as random effect and repeatability and among- and within-individual correlations between emergence time and time on the decoy were calculated as described above.

All multivariate mixed models were run with Gaussian error distributions. We set the number of iterations at 420,000, the burn-in phase at 20,000 and the thinning interval at 200. The results presented are from models with a non-informative parameter expanded prior (see Supplementary material for prior specification). The use of alternative prior specifications (i.e. Inverse Wishart and Inverse Gamma) gave qualitatively similar results. Traces of posterior distributions were checked visually and autocorrelation between successively stored iterations was less than 0.1 in all cases (Hadfield, 2010). Model convergence and mixing was assessed using Gelman Rubin statistics between chains (i.e. the potential scale reduction factor was <1.1 in all cases; Gelman & Rubin, 1992). Results presented are posterior mean estimates with associated 95% credible intervals (CrI), unless stated otherwise. Fixed-effect and correlation estimates were considered to find strong support if 95% CrI did not overlap with zero.

Results

Sources of (co)variation in aggression parameters

Repeatability of aggression parameters was low to moderate ($R_{\text{approach distance}}$ = 0.14 [0; 0.26], $R_{\text{number of calls}}$ = 0.33 [0.20; 0.45], $R_{\text{number of attacks}}$ = 0.28 [0.12; 0.46], $R_{\text{time decoy}}$ = 0.26 [0.11; 0.41]; see Table S1 for descriptive statistics on aggression parameters). On the among-individual level, we only found support for a correlation between the number of attacks and the time on the decoy (Table 1). On the within-individual level, all variables were correlated except for the number of attacks and the number of calls.

Emergence time and aggression

Repeatability of emergence time was high (R = 0.61 [0.54; 0.68]; see Table S1 for descriptive statistics on emergence time). Emergence time was affected by date. As the breeding season progressed females emerged later from their nest box relative to sunrise (Table 2). Time on the decoy was affected by age, with yearlings spending on average more time on the decoy than older females (Table 2). In 2019, females spend on average less time on the decoy than in 2018.

We found strong support for a negative among-individual correlation between emergence time from the nest box and time on the decoy. Females that consistently emerged earlier from the nest box spent consistently more time on the decoy compared to females that emerged later (r = -0.48 (-0.72; -0.25); Table 2; Figure 1A). On the within-individual level there was strong support for a correlation between emergence time and time on the decoy in the opposite direction. Specifically, an individual female was more aggressive when she emerged later, relative to her average emergence time, compared to when she emerged earlier (r = 0.35 (0.15; 0.53); Table 2; Figure 1B).

Discussion

To better understand the costs and benefits of among individual variation in chronotypes we investigated whether chronotype was part of a behavioural syndrome. More specifically, we studied whether chronotype was related to aggressive personality type in female great tits, as we expected that less aggressive females would benefit from an earlier onset of activity to avoid intra-specific competition. Contrary to our hypothesis, we found that females with an earlier onset of activity were consistently more aggressive. Intriguingly, we also found evidence for correlated plasticity between these two traits, i.e. a correlation at the within-individual level. Females were more aggressive when they emerged later relative to their average emergence time, and less aggressive when they emerged earlier. Below we discuss the possible causes of our findings from both a functional and mechanistic perspective.

During the territorial intrusion test we scored the approach distance, number of calls, time spent on the decoy and number of attacks. We used time on the decoy as proxy for aggression, which positively covaried both among- and within individuals with attacks, hence reflecting confrontational aggression. Notably, the correlations between the number of calls and the other behaviours were negative, both at the among- and within-individual level. Calling from a distance without physical contact might represent an alternative strategy to direct aggression in females, i.e. non-confrontational aggression (Thys et al. 2017; Boiten et al., 2023). However, this contradicts findings in male great tits, where the number of calls was positively correlated with the number of attacks and approach distance (Araya-Ajoy & Dingemanse, 2014; Samplonius, 2019). Yet, in blue tits, clear differences between same-sex aggression in males and females have been observed: females approached a female decoy closer, called much less, spent more time on the decoy and attacked more often than males when they were tested with a male decoy. Potentially, aggression in males and females may not be directly comparable due to their unequal investment in the nest (Boiten et al., 2023).

Females with an early onset of activity spent on average more time on the decoy, which contradicted our hypothesis that less aggressive personality types may benefit more from being early compared to more aggressive females, as it allows the former to avoid competition in a foraging context. The negative correlation between chronotype and aggressive personality type could possibly be explained by the fact that aggression correlates with risk-taking behaviour (Barnett et al., 2012; Bell & Stamps, 2004; Cain et al., 2011; Huntingford, 1976). Starting activity early could in turn be more risky as it might lead to higher levels of predation, since vision in great tits is impaired if light conditions are not optimal (Kacelnik, 1979). The negative among-individual correlation between chronotype and aggression thus potentially reflects differences in the level of risk-taking, representing a more extended behavioural syndrome.

On a mechanistic level, a negative relationship between chronotype and aggressive personality type could relate to differences among individuals in sex steroid concentrations or in the sensitivity to sex steroids (*sensu* the constraint hypothesis; Bell, 2005). Recent evidence has demonstrated that circadian rhythms are modulated by sex steroids and that the circadian clock has receptors for sex hormones (reviewed by Elderbrock et al., 2021). Notably, gonadotropin-releasing hormone-induced levels of estradiol are related to chronotype in female dark eyed juncos (*Junco hyemalis*), with individuals with higher peak levels of estradiol showing earlier chronotypes (Graham et al., 2019). Sex steroids may also affect aggression, although the exact mechanisms underlying this relationship are still not fully understood (Hau et al., 2000; Heimovics et al., 2015, 2018; Quintana et al., 2021; Soma, 2006; Soma et al., 2008). Furthermore, in the run-up to the breeding season, a period with great changes in sex steroid concentrations for both males and females, males tend to start activity progressively earlier in the morning than females (Schlicht & Kempenaers, 2020; Stuber et al., 2015), which may suggest that chronotype is regulated by sex hormones in male great tits too.

Additionally, genes that are involved in the circadian clock may have pleiotropic effects. For example, the CLOCK gene, which plays an important role in determining the circadian rhythm, is known to affect behaviour in mice (*Mus musculus*; Easton et al., 2003). Furthermore, mice that were selected for higher activity during the night were more aggressive and had altered expressions of genes that are involved in the circadian rhythm (i.e. CLOCK, PER1 and PER2; Kerman et al., 2012). The circadian rhythm of aggressive mice is also less sensitive to light and the period length in the absence of light is closer to 24h than that of less aggressive mice (Benus et al., 1988). Knocking out a circadian nuclear receptor (REV-ERBα) increased aggression in mice (Chung et al., 2014) and aggression levels showed circadian rhythms (Todd et al., 2018). Pleiotropic effects of sex steroids and gene expression could thus be promising targets for future research aiming to unravel the mechanistic underpinnings of the correlation between chronotype and aggressive personality type. Uncovering the proximate mechanisms driving this behavioural syndrome could, in turn, provide a more profound understanding of the functional consequences of chronotypes.

At the within-individual level we, however, found a positive correlation between emergence time and aggression, i.e. evidence for correlated behavioural plasticity (Pigliucci, 2003; Sheehy & Laskowski, 2023). It has been argued that suites of plastic behaviours may covary in response to a single factor, or to a set of environmental variables that covary itself (Sheehy & Laskowski, 2023). In our study system, one may argue that increased food availability may on the one hand allow individuals to spend more time in the nest box, thereby avoiding the high-risk twilight conditions, as they might need less time for foraging when conditions are favourable. On the other hand, patches with temporarily high food availability likely attract more conspecifics, and high social densities are known to increase aggression levels (Araya-Ajoy & Dingemanse, 2017; Quque et al., 2022; Yoon et al., 2012). Potentially, great tit females in our study plastically responded to two covarying environmental variables, i.e. food conditions and social density, with an orchestrated short-term change in both aggression and onset of activity. Such correlated behavioural plasticity in suites of behaviours is thought to be particularly beneficial in changing environments (e.g. Sih et al., 2011), but empirical evidence on the adaptive significance of these correlations is largely lacking. However, as behavioural traits are notoriously plastic, it will be essential to gain a better understanding of correlated behavioural plasticity in order to understand among-individual variation in behaviour. From a mechanistic viewpoint, pleiotropic effects, of which we argued above that they could give rise to behavioural syndromes are also likely to generate correlated plasticity (Dochtermann, 2023; Ellers & Liefting, 2015).

Our finding that the among-individual and within-individual correlation between emergence time and aggression are opposite could stem from their potential association with trade-offs in investment (Dochtermann, 2023; Downs & Dochtermann, 2014; Van De Pol & Wright, 2008). That is, within individuals, the allocation of available resources (such as energy) to one trait may come at the expense of another trait, but among individuals variation in individual quality or state may result in differences in overall resource acquisition (Laskowski et al., 2021). In the great tit, only high quality females might have enough resources available to invest in both aggression and early activity. In turn, increased aggression and earlier activity might also enhance resource acquisition, potentially, creating a positive feedback loop. At the within-individual level, the trade-offs could likely depend on the environmental conditions. During the egg-laying period, when emergence time and aggression were measured, resources are still limited and energy demands are high, due to the egg production. Trade-offs may therefore be more prominent when compared to less demanding or more favourable periods. These trade-offs could in principle generate opposing selection pressures, which can either imply that the rate of directional change may be low so that among others population (genetic) variation is maintained, or that it may require changes in the environment to resolve it. Yet, more research on the occurrence and significance of within-individual behavioural correlations is necessary to address this critical gap in our understanding. We currently know too little in order to provide conclusive answers.

Overall, our study provides evidence for the correlated expression of chronotype and aggression on the among-individual level, but whether this trait combination is adaptive and hence favoured by selection still needs to be shown. We found considerable variation among individuals in both behaviours, suggesting that the fitness consequences of this behavioural syndrome may be frequency dependent or could be related to fluctuating environmental factors, such as the food conditions and the social density. Considering the above mentioned studies in mice that demonstrated a mechanistic link between circadian clock characteristics and aggression (i.e. altered gene expression and the effect of knock-outs) it is plausible that the link between chronotype and aggression reflects an underlying shared mechanism, rather than being the result of correlational selection. Finally, when studying the functional consequences of variation in chronotypes and/or aggression, it is crucial to consider the proximate processes that could lead to their correlated expression both at the among- and within-individual level, as it is possible that they may not be able to evolve independently, potentially leading to suboptimal trait expression.

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Data availability

All data that support the findings of this study are provided as supplementary material.

Declaration of interest

The authors declare no conflict of interest.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve grammar and readability of some paragraphs. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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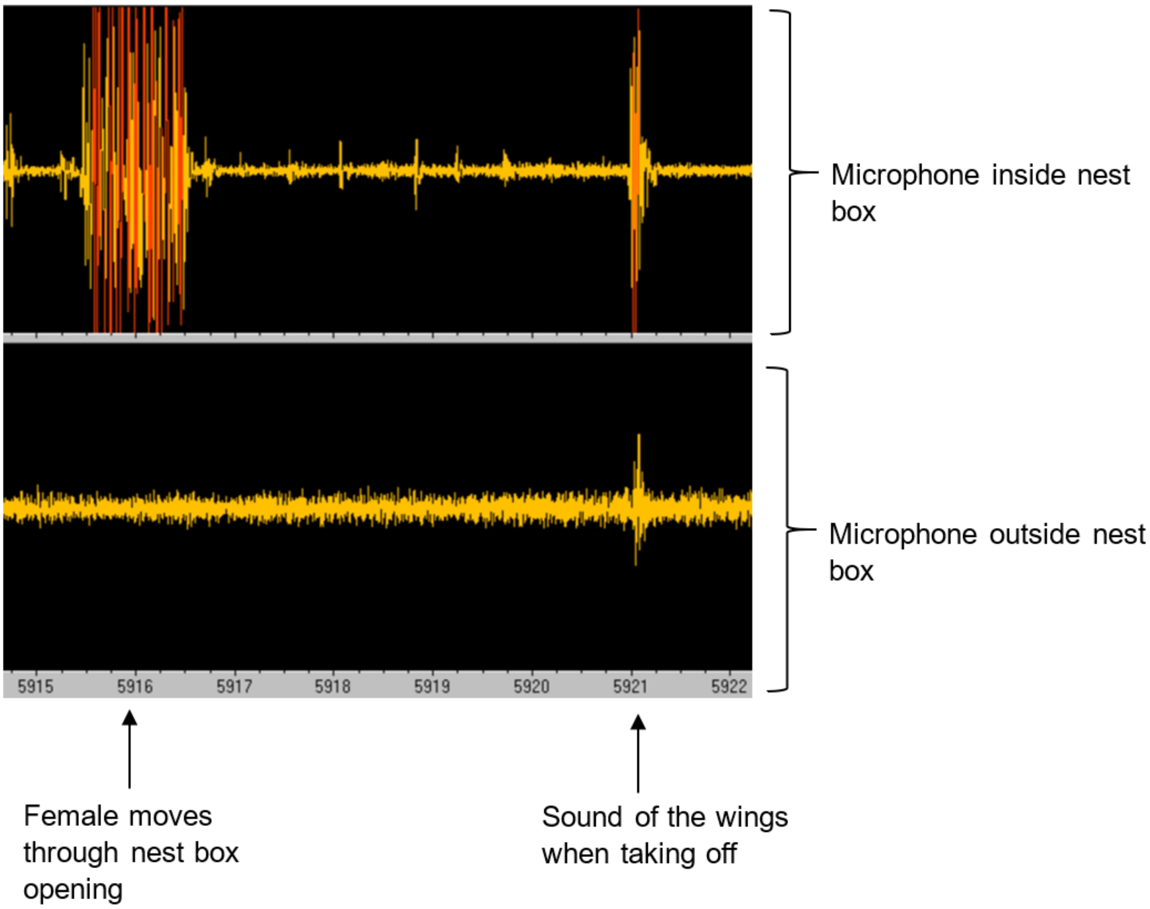
Appendix

Figure S1: audio graph created by Avisoft SASLab Pro 5.2.14, illustrating the emergence of a female from the nest box.



Prior specification for the multivariate mixed model with all aggression parameters

```
prior1 = list(R = list(V = diag(4), nu = 0.004),
              G = list(G1 = list(V = diag(4), nu = 4, alpha.mu = rep(0,4), alpha.V = diag(25^2,4,4,4))))
```

Prior specification for the multivariate mixed model with emergence time and time on the decoy

```
prior2 = list(R = list(V = diag(2), nu = 0.002),
              G = list(G1 = list(V = diag(2), nu = 2, alpha.mu = rep(0,2), alpha.V = diag(25^2,2))))
```

Table S1: descriptive statistics on the behavioural measurements during the territorial intrusion test and on emergence time.

	Mean	SD	Min	Max
Approach Distance	0.72	1.72	0	15
No. Calls	20.2	31.1	0	158
No. Attacks	3.0	7.7	0	61
Time Decoy	38.8	64.5	0	288
Emergence Time	8.4	16.9	-54	91

Tables

Table 1: Correlations (with 95% credible intervals) between the aggression parameters on the among-individual (above the diagonal) and within-individual level (below the diagonal).

	Approach distance	No. calls	No. attacks	Time decoy
Approach distance	-	- 0.12 (- 0.55; 0.35)	0.18 (-0.52; 0.72)	0.08 (-0.65; 0.65)
No. calls	**-0.16** **(-0.29; -0.04)**	-	-0.17 (-0.54; 0.23)	-0.17 (-0.52; 0.22)
No. attacks	**0.19** **(0.06; 0.32)**	-0.09 (-0.24; 0.05)	-	**0.85** **(0.63; 0.95)**
Time decoy	**0.38** **(0.26; 0.50)**	**-0.22** **(-0.36; -0.08)**	**0.79** **(0.73; 0.84)**	-

Table 2: Results from a bivariate mixed model with emergence time from the nest box (in minutes relative to sunrise) and time on the decoy (seconds) as response variables. Estimates of fixed (β) and random (σ^2) components are shown with 95% credibility intervals (CrI) and fixed effects that found strong support are given in bold.

	Emergence time	Time decoy
Fixed effects	β (95% CrI)	β (95% CrI)
Intercept	**0.18 (0.05; 0.33)**	**0.46 (0.30; 0.64)**
Year[a]	-0.15 (-0.29; 0.01)	**-0.33 (-0.52; -0.16)**
Age[b]	-0.19 (-0.36; 0.00)	**-0.68 (-0.90; -0.47)**
Date[c]	**3.61 (0.08; 7.14)**	-3.11 (-7.47; 1.48)
Date 2[c]	**5.13 (2.01; 8.07)**	-3.96 (-8.81; 0.92)
T° at sunrise[d]	-0.01 (-0.03; 0.02)	-
Random effects	σ^2 (95% CrI)	σ^2 (95% CrI)
FemaleID	0.61 (0.47; 0.76)	0.31 (0.16; 0.48)
Residual	0.38 (0.34; 0.43)	0.65 (0.52; 0.78)
$\text{Cov}_{\text{among individuals}}$	-0.21 (-0.33; -0.10)	-
$\text{Cov}_{\text{within individuals}}$	0.17 (0.07; 0.27)	-
$\text{Cor}_{\text{among individuals}}$	-0.48 (-0.72; -0.25)	-
$\text{Cor}_{\text{within individuals}}$	0.35 (0.15; 0.53)	-
Repeatability	0.61 (0.54; 0.68)	0.32 (0.19; 0.47)

[a] 2018 is used as reference year

[b] Yearling is used as reference age

[c] Date of measurement mean centred within years

[d] Temperature at sunrise mean centred within years

Figure legend

Figure 1: Correlation between emergence time from the nest box and time spent on the decoy during a simulated territorial intrusion in female great tits (N = 181) at the among-individual level (A) and the within-individual level (B). BLUPs were extracted from a bivariate mixed model (Table 2) and used here for illustrative purposes only (Houslay & Wilson, 2017). The within-individual effect was visualised by mean-centring the data within individuals for both emergence time and time on decoy.