BRILL Behaviour (2018) DOI:10.1163/1568539X-00003522 Behaviour brill.com/beh

Consistent individual and sex-specific differences in behaviour of common cuckoo chicks: is there a potential impact on host-parasite coevolutionary dynamics?

Alfréd Trnka [a,*], **Peter Samaš** [b] and **Tomáš Grim** [c]

[a] Department of Biology, University of Trnava, Priemyselná 4, 918 43, Trnava, Slovakia
[b] Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Květná 8, 60365 Brno, Czech Republic
[c] Department of Zoology and Laboratory of Ornithology, Palacký University, 17. listopadu 50, 77146 Olomouc, Czech Republic
[*]Corresponding author's e-mail address: atrnka@truni.sk

Received 20 August 2018; initial decision 15 September 2018; revised 30 September 2018; accepted 3 October 2018

Abstract

Research on brood parasitism has focused primarily on specific host anti-parasite behaviours and parasite counter-adaptations, and little is known about other aspects of their behaviours such as consistent behavioural differences between individuals. Therefore, we examined consistency in behaviour of nestlings of common cuckoos (*Cuculus canorus*) raised by great reed warblers (*Acrocephalus arundinaceus*). Cuckoo chicks showed high repeatability of both aggressive behaviour and breath rate, and both traits were strongly correlated with each other. This represents the first evidence for consistent differences in behaviour among avian brood parasites. Males were consistently more aggressive and less stressed than females. Nestlings of both sexes that hatched later in the season exhibited higher levels of aggression and lower stress responses than nestlings hatched earlier. This suggests that rearing conditions (e.g., food availability and quality) may modulate stress and aggressive phenotypes of brood parasites. We discuss potential effects of the observed patterns on host-parasite dynamics.

Keywords

breath rate, common cuckoo, great reed warblers, handling aggression, behavioural consistency.

DOI 10.1163/1568539X-00003522

1. Introduction

Obligate interspecific brood parasitism in birds (i.e., when females lay their eggs in the nests of other species leaving them to raise their nestlings) constitutes one of the best-known examples of coevolution in vertebrates and has been the subject of many studies in behavioural ecology and evolutionary biology (Rothstein, 1990; Davies, 2000; Soler, 2017). Most research on avian brood parasitism has therefore focused primarily on specific host anti-parasite behaviours (discrimination of parasite eggs, young and adults) and both parasite behavioural and morphological counter-adaptations (mimicry in parasite eggs, young and adults; reviewed in Soler, 2017). In contrast, little is known about the role of those traits that did not evolve specifically during parasite-host coevolution but still could influence the coevolutionary dynamics (general life-history traits sensu Grim et al., 2011). Such traits have been so far studied very little and almost exclusively in the common cuckoo (*Cuculus canorus*, hereafter: cuckoo) (egg-laying at two days intervals: Davies, 2000; internal incubation: Birkhead et al., 2011; nestling repulsive secretions: Trnka et al., 2016) and its hosts (mating system: Trnka & Prokop, 2011; nest cup design: Grim et al., 2011; clutch size: Hauber et al., 2014; nestling diet: Grim et al., 2017).

One such largely neglected aspect of brood parasite and host behaviours is consistent behavioural differences between individuals or personality (Avilés & Parejo, 2011). There is growing evidence that individual animals, including birds, differ consistently in their behaviour among each other (i.e., they exhibit a personality) and that these differences can covary with other repeatable traits, either behavioural or states (behavioural syndrome and pace-of-life syndrome: Sih et al., 2004; Réale et al., 2010). For example, some individuals are consistently more aggressive or bolder than other individuals and aggressive individuals are also bold in different contexts or situations (Verbeek et al., 1996; Dingemanse et al., 2007; Hollander et al., 2008). In addition, such personality traits and traits' correlations can be heritable and may have important fitness consequences (Dingemanse et al., 2002, 2004; van Oers et al., 2005; Smith & Blumstein, 2008).

In accordance with this conception, some recent theoretical and empirical studies have suggested that such behavioural differences between individuals may predict the susceptibility of individual hosts to brood parasitism and variation in their anti-parasite behaviour (Avilés & Parejo, 2011; Guigueno & Sealy, 2011; Samaš et al., 2011; Avilés et al., 2014; Grim et al., 2014a;

Trnka & Grim, 2014). Specifically, bold or more aggressive host individuals are more likely to defend their nests against adult brood parasites (Trnka & Grim, 2014) and reject parasitic eggs more often than shy or less aggressive hosts (Avilés et al., 2014; but see Trnka & Grim, 2014). Such individuals, on the other hand, may be more prone to being parasitized because they are also more active and, thus, expose themselves more to brood parasites than shy host individuals (cf. nesting-cue hypothesis, Robertson & Norman, 1977). Other behavioural traits that may relate to specialized host defences and influence the risk of brood parasitism are exploratory behaviour, aggressiveness against conspecifics and sociability (Avilés & Parejo, 2011).

However, not only hosts but also brood parasites may exhibit consistent differences in their behaviour that could affect the likelihood of successful brood parasitism. For example, bold and aggressive brood parasite females would be expected to be more successful at parasitizing the nests of more aggressive hosts than shy and non-aggressive parasite females. On the other hand, shy and non-aggressive parasites with less conspicuous behaviour could be more effective at parasitizing the nests of good egg discriminators because sight of a brood parasite near host nest facilitates egg discrimination by hosts (Moksnes et al., 2000; Požgayová et al., 2009; see also Hanley et al., 2015). As shown earlier, selection on aggressive behaviour might also result in a positive feedback between an increasingly retaliating (mafia-like) parasite and ever more compliant host behaviours (Soler et al., 1995; Hoover & Robinson, 2007).

Similarly, in brood parasitic nestlings, an individual's personality traits can affect the dynamics of its interactions with foster parents and step-siblings (in the case of non-evictor brood parasite species: Hauber & Ramsey, 2003), thereby influencing the amount of food received and, consequently, its growth, survival and fitness. Importantly, nestling behavioural traits could be also used as a predictor of an individual's future adult personality (McCowan & Griffith, 2014; but see Fucikova et al., 2009). Nevertheless, in contrast to host personality or behavioural syndrome (Avilés & Parejo, 2011; Trnka & Grim, 2014; Avilés et al., 2014), no studies have so far examined consistent individual differences in behaviour of obligate brood parasites (including their nestlings: Grim, 2007a) and their role in the host-parasite dynamics.

Here we made the initial step to fill this gap. We investigated two behavioural responses (aggression and breath rate during handling) in the nestlings of the common cuckoo raised alone in the nests of the great reed warbler (*Acrocephalus arundinaceus*) hosts. The limited number of behavioural assays and measurements are trade-offs between data strength and experimental context (natural *vs* laboratory conditions, for more details see Material and methods). Handling aggression and breath rate are widely accepted and commonly used behavioural traits in studies of behavioural correlations in birds, including their nestlings (Carere & van Oers, 2004; Fucikova et al., 2009; Brommer & Kluen, 2012; but see David et al., 2012), where breath rate, although it is not a true personality trait by definition, is generally considered a good predictor of personality and by some authors even accepted as a personality trait (e.g., Class & Brommer, 2015). Moreover, breath rate represents also an important indicator of acute physiological stress response (van Oers et al., 2015).

We first tested whether handling aggression and breath rate are statistically repeatable and correlate with each other and thus reflect consistent individual differences in behavioural responses of cuckoo nestlings to handling. Given that intersexual differences in life-history and sexual selection pressures can lead to sex differences in behavioural traits and their correlations (Schuett et al., 2010; Fresneau et al., 2014), we further examined whether there are also differences between male and female cuckoo nestlings in their behavioural responses. To our knowledge, only a single study focused so far on sex differences in cuckoo nestling behaviour (begging and pecking) but did not find any (Abraham et al., 2015). We predicted that (a) nestling males are due to their bigger size (Glutz von Blotzheim & Bauer, 1980; Požgayová et al., 2018) and generally higher levels of testosterone (Wingfield et al., 1987; Soma, 2006) consistently more aggressive than nestling females and, on the contrary, (b) they will exhibit lower responses to handling stress than females since negative correlation between handling aggression and breathing rate was found in nestlings of other avian species (Brommer & Kluen, 2012).

2. Material and methods

2.1. Study sites and general field procedures

The study was conducted in 2016 and 2017 at seven localities in the Podunajská nížina lowland, SW Slovakia: three fishpond systems near Štúrovo (47°51′N, 18°36′E), Trnava (48°21′N, 17°33′E) and Horná Krupá (48°29′N, 17°32′E), one gravel pit near Majcichov (48°16′N, 17°39′E), one small water reservoir near Jatov (48°08′N, 18°01′E) and two canals near Komárno

(47°47′N, 18°00′E and 47°49′N, 18°00′E). The distances between these localities ranged from 5 to 97 km. Detailed descriptions of the most of them are available elsewhere (Prokop et al., 2009; Trnka et al., 2009, 2010, 2013; Trnka & Prokop, 2010). The number and position of localities as well as the year of the study (each locality was sampled in only one year) were selected in order to reduce the probability of kinship relationships among tested cuckoo nestlings as handling aggression and breath rate are known to be heritable in some bird species (Class et al., 2014). Such spatial metareplication should also lead to stronger conclusions than any single study site study could in principle (see, e.g., Grim et al., 2011).

From May to late July, we searched littoral vegetation for the parasitized nests of the great reed warbler that is the main cuckoo host in the study sites. Successfully parasitized nests (i.e., nests where a cuckoo egg had been accepted by hosts) were monitored daily around the expected hatching date to accurately determine the age of cuckoo nestlings. Thereafter, we did not visit the nests until behavioural measurements. Thus, cuckoo nestlings were not influenced by our research activity before the experiment was performed (cf. Hanley et al., 2015). Out of 67 nests with accepted cuckoo eggs, 11 nests were predated during the incubation period and 15 failed due to other reasons during the incubation or nestling stages. Thus, in total we tested 41 cuckoo nestlings (22 males and 19 females).

Given that blood collection for DNA sexing can cause additional stress in avian nestlings (van Oers & Carere, 2007), tested chicks were sampled after all behavioural measurements were taken. We took 3–5 small drops of blood from nestlings' medial metatarsal vein and preserved it in 70% ethanol. Subsequent sex determination was performed in the private accredited genetic laboratory Genomia (https://www.genomia.cz/en/).

We conducted the first handling tests on 15–16 days old cuckoo nestlings (hatching day = 0) and, to be able to estimate the statistical repeatability of behavioural traits, we repeated measurements on each individual nestling 3 days later. This relatively short time interval between the two trials was limited by ontogeny and fledging time of cuckoo nestlings. However, similar intervals between consecutive measurements have been also successfully applied in other studies on avian chicks (see, e.g., Krams et al., 2014; McCowan & Griffith, 2014; Karlíková et al., 2018). Both ages were suitable for carrying out such tests in this species as nestling stress and aggressive self-defence responses are fully developed after the age of two weeks post-hatch and nestlings are already fully feathered (Mikulica et al., 2017; pers. obs.) and in the asymptotic phase of their growth (Kleven et al., 1999; Grim & Samaš, 2016; Li et al., 2016). During the second set of measurements nestlings were already shortly before fledging: cuckoo nestlings fledge from great reed warbler nests when about 18–21 days old (own data; see also Kleven et al., 1999; Grim & Samaš, 2016; Li et al., 2016). However, there are low risks of inducing premature fledging (in contrast to host nestlings: Grim, 2007b) because cuckoo chicks are passive and can be safely handled until fledging (own field experience from handling cuckoo nestlings in various host species, including great reed warblers: Grim, 2006; Grim et al., 2011, 2014b, 2017; Grim & Samaš, 2016; Li et al., 2016; Trnka et al., 2016; Mikulica et al., 2017) and even after fledging (up to three days post-fledge: Tyller et al., 2018) without inducing an escape response.

2.2. Handling aggression and breath rate

We started the handling aggression test by gently grabbing and removing the cuckoo nestling from the host nest. Immediately after removal, we weighed each nestling with a Pesola spring balance to the nearest 0.1 g. The entire procedure (grabbing, removing and handling) took about 5 min. During this period we scored the nestling's response to being handled on an interval scale ranging from 1 (an individual is completely passive) to 5 (an individual struggles continuously) (following Brommer & Kluen, 2012).

After handling, we put the nestling into a cloth bag where it was kept for 5 min to stabilise its respiratory rate (see also Torne-Noguera et al., 2014). Thereafter, we carefully removed it from the bag, fixed in hand (following Fucikova et al., 2009) and measured time that passed during 30 breaths by the cuckoo nestling with a stopwatch for two consecutive times (Brommer & Kluen, 2012). We then calculated breath rate (number of breaths per 1 s) as the average of these two measurements.

All tests were performed by the first author (AT). All tested nestlings successfully fledged from their nests.

2.3. Statistical analyses

2.3.1. Within-trait repeatability

We calculated adjusted within-trait repeatability (Nakagawa & Schielzeth, 2010) using univariate models with the package lme4 (Bates et al., 2015) for the trait "breath rate" (linear mixed-effects model) and package ordinal

(Christensen, 2018) for “handling aggression” (ordered logit mixed-effects models) using software R v. 3.5.0 (R Development Core Team). Full models contained fixed predictors: “nestling sex” (binary, male and female), “date” of experiment (continuous; 1 = 1st May), “daytime” (continuous, hour), ambient “temperature” (continuous, in °C), “mass” (continuous) and interaction of “nestling sex” and “mass”. We controlled for repeated measures of the same individual by including “nestling ID” as a random intercept. Predictors involved in interactions were centred around their means to make biologically lower order predictors interpretable (Schielzeth, 2010). Potential collinearity among the covariates was satisfactory: variance inflation factors were <1.8 for all predictors (Zuur et al., 2010).

We used stepwise regression with backward elimination of statistically non-significant predictors to create the final models (Grafen & Hails, 2002). However, we present outputs of both the full (with all predictors) and final reduced models because different statisticians recommend either the former or the latter approach (Forstmeier & Schielzeth, 2011; Grafen & Hails, 2002, respectively). Adjusted repeatability from the final linear model was calculated as the between-individual variance divided by the sum of the between-individual and within-individual variance (Nakagawa & Schielzeth, 2010). Adjusted repeatability from the final ordered logit model was calculated by the formula $r = \mathrm{VB}/(\mathrm{VB} + \mathrm{VE} + \pi 2/3)$, where VB is between-group variance, VE is the residual variance fixed to 0, and $\pi 2/3$ is the inherent distribution-specific variance (Nakagawa & Schielzeth, 2010). The asymptotic 95% confidence intervals for the repeatability estimates from the mixed-effects models were calculated using the package psych (Revelle, 2018).

2.3.2. *Between-trait correlations*

We employed the Bayesian multi-response mixed-effects model (package MCMCglmm, Hadfield, 2010) to estimate the covariance between the both repeatable behavioural traits at the individual level. The response of “breath rate” was modelled as Gaussian (link identity) and “handling aggression” as ordinal (link probit, family threshold). We included fixed predictors of “nestling sex” and experimental “date” as both were statistically significant in previous within-trait repeatability analyses. We again included “nestling ID” as a random intercept effect to control for repeated measures. We set an uninformative flat prior and ran 1×10^5 iterations with a burn-in phase of 3000 and a thinning interval of 10 to obtain >9000 effective samples per parameter for posterior inference. We fitted an unstructured covariance matrix for the grouping effect “nestling ID” and fixed residual variance associated with categorical response “handling aggression” to 0. From the model output, we obtained a posterior distribution for between-trait covariance and standardized it to get a correlation estimate with 95% credible intervals. We obtained empirical like p-value from posterior samples to test significance for the fixed effects “nestling sex” and “date” across both response variables. For this purpose, we used Wald test (package aod v. 1.3, Lesnoff & Lancelot, 2012), which uses predictor posterior mean and posterior covariances to calculate chi-square value with p-value. Simulations showed that such test of predictor effect under multi-response method is superior to corresponding univariate tests (Ruotsalainen, 2017).

2.4. *Ethical notes*

We followed guidelines of the Animal Behaviour Society for the ethical use of animals in research. Licences and permission to handle the birds and to perform the experiments were provided by the Ministry of Environment of the Slovak Republic. When locating and checking great reed warbler nests we moved slowly through the reeds trying to avoid damaging reed stems and disturbing breeding birds or attracting potential nest predators. According to our previous experience (e.g., Trnka et al., 2016, 2018) we are also sure that our field experiments did not negatively affect survival of cuckoo nestlings.

3. Results

Cuckoo nestlings ($N = 41$) showed high within-trait repeatability for both behavioural traits, i.e., handling aggression and breath rate (Table 1, Figure 1). Correlations among the two traits were high with a negative relationship between breath frequency and handling aggression (Table 1, Figure 1), controlling for significant effects of nestling sex ($\chi^2 = 19.3$, $p < 0.0001$) and experimental date ($\chi^2 = 29.6$, $p < 0.0001$).

In comparison to female cuckoo nestlings ($N = 19$), male cuckoo nestlings ($N = 22$) had lower breath rate (Table 2, Figure 2) and were more aggressive during handling than females (Table 3, Figure 2). In both sexes, as the season progressed, breath rate decreased (Table 3) whereas handling aggression increased (Table 2). Furthermore, higher body mass was associated with increased handling aggression in male cuckoos while females’ aggression decreased with their increasing mass (Table 3).

Table 1.
Correlation estimates within and between two behavioural traits in common cuckoo nestlings and (co)variance components used for their calculation (see Statistical analyses for details).

Trait	*r* (95% CI)	Component	Estimate (95% CI)
Breath rate	0.96 (0.92, 0.98)	Intercept variance	0.029 (0.017, 0.045)
		Residual variance	0.0013 (0.0008, 0.0020)
Handling aggression	0.75 (0.49, 0.88)	Intercept variance	9.679 (2.865, 17.676)
		Residual variance	–
Breath rate *vs* handling aggression	−0.75 (−0.89, −0.58)	Covariance	−0.134 (−0.240, −0.079)
		Breath variance	0.024 (0.016, 0.041)
		Handling variance	1.338 (0.878, 2.170)

r values represent within-trait adjusted repeatabilities for traits "breath rate" and "handling aggression" and between-trait standardized covariance for "breath rate *vs* handling aggression". For the adjusted repeatabilities, the variances (presented with their 95% confidence intervals) were calculated using frequentist univariate mixed-effects models. For the between-trait correlation, (co)variances (presented with their 95% credible intervals) were calculated using Bayesian multi-response mixed-effects model (see Statistical analyses).

4. Discussion

We found that aggression and breath rate during handling were highly repeatable and correlated with each other in common cuckoo nestlings. Additionally, we detected statistically significant differences in behaviour of cuckoo nestlings based on their sex: compared to females, males were more aggressive and showed less stress as evidenced by their breath rate. These sexual differences also showed contrasting covariation with other traits between the two sexes: heavier males were more aggressive whereas heavier females showed decreased aggression. These results provide the first empirical evidence for the consistent individual and sex-specific differences in behaviour among brood parasites.

4.1. Behavioural consistency

High repeatability of the two behavioural traits indicates their high short-term consistency. However, given that repeatability of any behaviour is known to decrease with the length of an interval between the consecutive measurements (Bell et al., 2009; Grim et al., 2014a), results do not allow us to assess to what extent (if at all) breath rate and handling aggression are individually consistent later in life, i.e., in fledglings and adults.

Moreover, due to relatively high behavioural plasticity in young animals, differences among adult individuals may often be blurred (Polverino et al.,

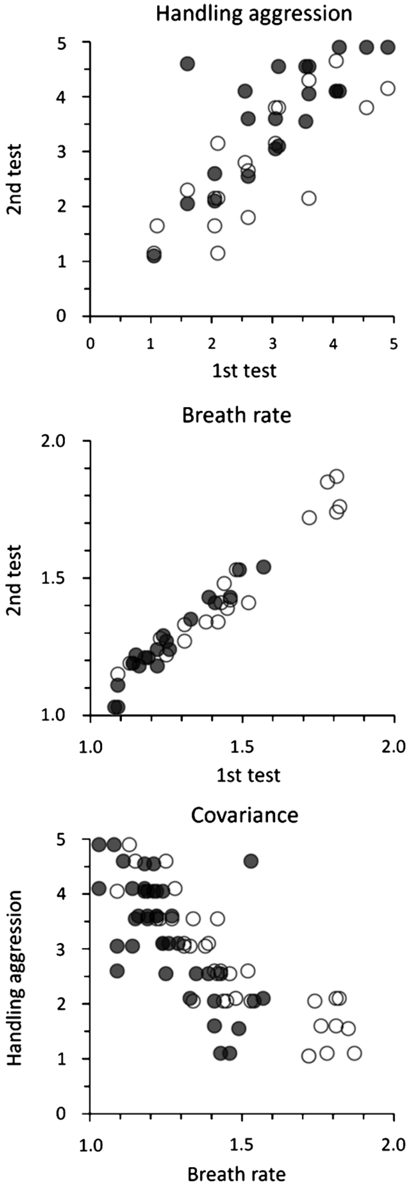

Figure 1. Scatterplots of within-trait covariance between the first and second test for the two tested behavioural traits and their between-trait covariance in parasitic common cuckoo nestlings (females: $N = 19$, open circles; males $N = 22$, closed circles). Handling aggression was measured on an ordinal scale (see Material and methods for details), breath rate is expressed as the number of breaths per second.

Table 2.
Outputs of full and final reduced models explaining variation in breath frequency in common cuckoo nestlings (continuous response variable).

Predictor	Full model ($R^2_m = 0.36$, $R^2_c = 0.97$, $AIC_c = -82.9$)			Final model ($R^2_m = 0.35$, $R^2_c = 0.97$, $AIC_c = -128.8$)		
	F	p	Estimate ± SE	F	p	Estimate ± SE
Intercept	–	–	1.76 ± 0.16	–	–	1.79 ± 0.13
Sex (F)	16.5	0.0002	-0.22 ± 0.05	16.1	0.0003	-0.22 ± 0.05
Date	6.1	0.02	-0.007 ± 0.006	6.3	0.01	-0.006 ± 0.002
Daytime	1.2	0.37	0.007 ± 0.006	–	–	–
Temperature	0.1	0.59	-0.001 ± 0.002	–	–	–
Mass	0.9	0.34	0.001 ± 0.003	–	–	–
Sex × mass	0.2	0.23	0.002 ± 0.004	–	–	–

Model fits are summarized using marginal (R^2_m) and conditional (R^2_c) R-squared accompanied with AIC_c (Nakagawa & Schielzeth, 2013). (F), female as the reference level of the predictor.

2016a,b). Although some studies suggested that nestling behaviour can be predictive of future adult phenotype (McCowan & Griffith, 2014), there is mixed evidence for the consistency of behaviour over the ontogeny (reviewed in Wuerz & Krüger, 2015), and a number of studies showed many

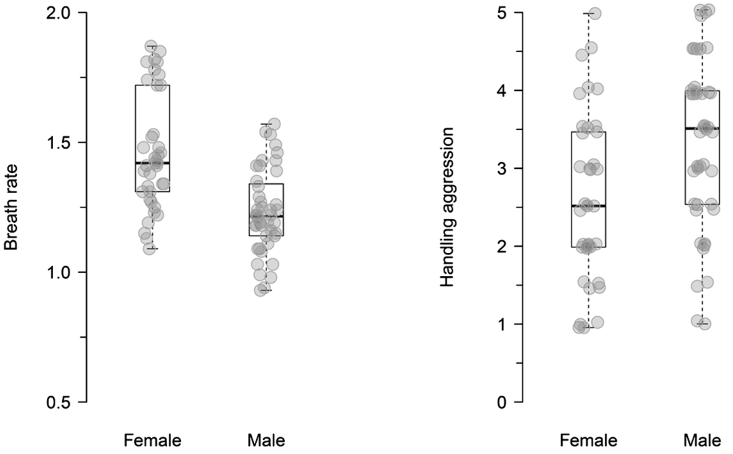

Figure 2. Sex-related differences in breath rate (number/s) and handling aggression (ordinal scale, see Material and methods for details) in female ($N = 19$) and male ($N = 22$) common cuckoo nestlings.

Table 3.

Outputs of full and final reduced models explaining variation in handling aggression in common cuckoo nestlings (ordinal response, see Methods for details). "[F]" = female as the reference level of the predictor.

Predictor	Full model ($AIC_c = 335.1$)			Final model ($AIC_c = 332.9$)		
	χ^2	p	Estimate ± SE	χ^2	p	Estimate ± SE
Sex (F)	3.89	0.049	2.17 ± 1.11	4.17	0.041	2.26 ± 1.12
Date	9.36	0.002	0.19 ± 0.07	9.04	0.003	0.19 ± 0.07
Daytime	0.15	0.70	0.13 ± 0.33	–	–	–
Temperature	1.8	0.18	0.15 ± 0.11	–	–	–
Mass	0.1	0.81	−0.20 ± 0.15	0.1	0.81	−0.21 ± 0.14
Sex × mass	4.8	0.03	0.43 ± 0.21	4.8	0.03	0.43 ± 0.21

behavioural traits including breath frequency to change across an individual's lifespan (Dingemanse et al., 2010; Class & Brommer, 2016; Favati et al., 2016; Polverino et al., 2016a). Therefore, further research should focus on similar behavioural assessments on longer time-scales in order to determine whether different selection pressures on juvenile and adult cuckoos could lead to individual differences in tested traits (Stamps & Groothuis, 2010a).

4.2. Sex differences

Interestingly, we found males to be consistently more aggressive and less stressed during handling than females indicating the sex-specific susceptibility to acute stress in cuckoo chicks. Although previous studies have also found that aggressive or bold birds tend to be less susceptible to handling stress (Carere & van Oers, 2004; Brommer & Kluen, 2012), none of them have shown intersexual differences in these tendencies in nestlings.

Observed differences can be determined environmentally, genetically (genetic differences between males and females), or maternally (sex-specific allocation of maternal hormones to eggs: Groothuis et al., 2005; Eising et al., 2006; von Engelhardt et al., 2006). The differences may result from different selection pressures on males and females associated with their different roles in the brood parasitic breeding strategy (Schuett et al., 2010). Note that only cuckoo females seek and choose host nests for parasitism (Wyllie, 1981), whereas males' reproductive success depends mainly on the number of females that they mate with and their ability to keep other males away from potential mates. Hence, more aggressive males should be more successful in occupying and defending large territories, and so, in mating with more females as well. Our results suggest that these potential sex differences in adults (yet to be tested) can originate already in young cuckoos.

In contrast, a previous study on the behaviour of cuckoo nestlings have found no sexual differences in other behavioural traits such as begging vocalization and the number of pecks directed at host parents (Abraham et al., 2015). Similarly, male and female nestlings did not differ in their pecking behaviour directed towards the researcher in our preliminary study (results not shown). Sample sizes were only slightly smaller ($N = 15$ per sex) in the study of Abraham et al. (2015) than in the present study (N approximately 20 per sex); thus, the power of the tests alone is an unlikely explanation for these differences.

One explanation for the differences may be that begging represents a behaviourally completely different behavioural trait compared to aggression during handling and breath rate (see also Trnka & Grim, 2014). Specifically, nestling begging is motivated to elicit the food intake whereas handling aggression represents an immediate response to threat. It is likely that begging is more variable and plastic compared to aggression and breath rate because begging reflects immediate chick hunger (which is necessarily highly variable) whereas stress-related traits reflect self-defence (which should be less variable as a choice between self-preservation and death); if that is true than the higher variation (i.e., lower repeatability) in begging, coupled with slightly smaller sample sizes (see above), would not allow to statistically detect any sex-specific differences in begging even if they existed. The sex-specific differences in begging are likely because cuckoo males reach higher asymptotic mass than females (Požgayová et al., 2018) and this would be hard to explain if there were not any differences in food intake which implies differences in begging too. Indeed, nestling cuckoo males tend to be fed more than cuckoo females (Figure 2d in Abraham et al., 2015) although the difference did not reach conventional statistical significance. However, cuckoo nestlings were not tested for the repeatability of their begging behaviour by Abraham et al. (2015) which provides an impetus for more research in this area.

4.3. Seasonal patterns

Cuckoo nestlings of both sexes that hatched later in the season exhibited higher levels of aggression and lower reactions to handling stress than nestlings hatched earlier. Given that not only genetic but also environmental factors can contribute to the expression and development of behavioural traits (Groothuis & Carere, 2005; Stamps & Groothuis, 2010b), observed seasonal patterns in the cuckoo nestling behaviour could also be caused by potential changes in concentrations of maternal hormones transferred to cuckoo egg yolks over the laying sequence (Groothuis et al., 2008).

Indeed, cuckoo females lay their eggs at two-day intervals and a single female may produce as many as 15 eggs in a season (up to 25 eggs: Wyllie, 1981), i.e., their egg laying process takes around 30 days (or even more) (as also suggested from cuckoo migration patterns: Willemoes et al., 2014). Thus, if yolk hormones, such as androgens or corticosterone (the main stress hormone in birds: Palme et al., 2005), decrease over the laying sequence, then cuckoo nestlings hatched later in the season should also exhibit lower levels of stress (lower rate of breathing) than nestlings hatched earlier in the season. However, previous studies on hormonal levels in cuckoos either did not test for seasonal effects (Török et al., 2004; Igic et al., 2015) or did not find any effects of date in the season (Hargitai et al., 2012).

Additionally or alternatively, seasonal behavioural patterns might reflect seasonal changes in the amount and quality of food delivered by foster parents to cuckoo nestlings (Grim et al., 2017). Several previous studies have confirmed that nestlings of altricial birds provisioned with lower amounts of some types of food (mainly caterpillars and spiders) have a stronger stress response than nestlings that received larger quantities of the same food type (Arnold et al., 2007; van Oers et al., 2015). Cuckoo nestling diet varies strongly and consistently both among host species (Grim & Honza, 2001; Martín-Gálvez et al., 2005; see also Tyller et al., 2018) and among host pairs (within a single host species: Grim et al., 2017) and differs consistently from diet delivered to host nestlings (Grim & Honza, 2001; Martín-Gálvez et al., 2005). However, according to Abraham et al. (2015), the amount of food brought to cuckoo nestling by great reed warbler foster parents decreased significantly as the breeding season progressed, regardless of the nestling mass (but see Grim et al., 2017). We therefore suggest that not the amount of food, but rather a specific type of food available later in the season should have more influence on expression of behavioural traits we tested.

Handling aggression was positively correlated with the mass of male (but not female) cuckoo nestlings in our study suggesting different potential effects of food on nestling behaviour in males and females. However, previous studies of cuckoo nestling growth did not consider nestling sex (reviewed in Grim, 2006; Grim & Samaš, 2016; but see Požgayová et al., 2018). Therefore, and given that other environmental factors can also contribute to observed patterns, additional experimental evidence is needed to test above mentioned explanations. Nevertheless, results should still be interpreted with caution because although breath rate is considered a reliable proxy of the physiological response of birds to acute stress (Carere & van Oers, 2004; Fucikova et al., 2009; van Oers et al., 2015), measuring the frequency of respiratory acts in small species has some limitations (Fučíková et al., 2009; Torné-Noguera et al., 2014; Trnka et al., 2018). Hence, given that any stress response typically involves the activation of endocrine mechanisms, mainly secretion of glucocorticoid hormones such as corticosterone that boost energy availability to respond appropriately to a given stress, future studies examining baseline corticosterone levels of individual nestlings and their ability to release this hormone in response to handling will be necessary.

4.4. Conclusions

The findings on the consistency and sex-specific differences in aggressive and stress responses to repeated handling in the common cuckoo nestlings have important theoretical, as well as practical implications. Future studies should address the question whether aggression and stress responses of cuckoo nestling to handling may extend to other behavioural traits and whether it is influenced by diet fed to cuckoo nestlings. Given that early rearing environment such as food availability can have significant effect on behaviour of animals later on in their lives (van Oers et al., 2015; Langenhof & Komdeur, 2018), the quality of the hosts in terms of provisioning behaviour may also influence the behavioural phenotype of adult cuckoos: e.g., some great reed warbler hosts feed cuckoo nestlings with vertebrate diet, namely small mammals, fish and amphibians (Trnka, 1995; Mikulica et al., 2017). Thus, consistent behavioural differences in both young and adult cuckoos would affect the dynamics of coevolutionary arms-race between avian brood parasites and their hosts just like the host consistent behaviour has already been documented to have important effects on parasite fitness (Avilés et al., 2014; Grim et al., 2017). Therefore, addressing these topics experimentally is a major challenge for future studies. On the other hand, sex-specific susceptibility to handling stress in cuckoo nestlings and potential long-term behavioural and physiological effects of exposure to such manipulations (van Oers & Carere, 2007) should also be taken into methodological considerations in studies of behaviour in the common cuckoo and potentially other brood parasite species nestlings.

Acknowledgements

We thank M. Trnka and B. Trnková for their assistance in the field. We also thank two anonymous referees for their helpful comments. Fishpond keepers allowed us to work in private fishpond areas. During the work on the manuscript, PS was supported by the Czech Science Foundation (grant 17-12262S). Access to computing and storage facilities owned by parties and projects contributing to the National Grid Infrastructure MetaCentrum provided under the programme "Projects of Large Research, Development, and Innovations Infrastructures" (CESNET LM2015042), is greatly appreciated.

References

Abraham, M., Požgayová, M., Procházka, P., Piálková, R. & Honza, M. (2015). Is there a sex-specific difference between parasitic chicks in begging behaviour? — J. Ethol. 33: 151-158.

Arnold, K.E., Ramsay, S.L., Donaldson, C. & Adam, A. (2007). Parental prey selection affects risk-taking behavior and spatial learning in avian offspring. — Proc. Roy. Soc. Lond. B: Biol. Sci. 274: 2563-2569.

Avilés, J.M. & Parejo, D. (2011). Host personalities and the evolution of behavioral adaptations in brood parasitic-host systems. — Anim. Behav. 82: 613-618.

Avilés, J.M., Bootello, E.M., Molina-Morales, M. & Martinez, J.G. (2014). The multidimensionality of behavioural defences against brood parasites: evidence for a behavioural syndrome in magpies? — Behav. Ecol. Sociobiol. 68: 1287-1298.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Eigen, C. & Rcpp, L. (2015). Package 'lme4'. — R Foundation for Statistical Computing, Vienna.

Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009). The repeatability of behaviour: a meta-analysis. — Anim. Behav. 77: 771-783.

Birkhead, T.R., Hemmings, N., Spottiswoode, C.N., Mikulica, O., Moskát, C., Bán, M. & Schulze-Hagen, K. (2011). Internal incubation and early hatching in brood parasitic birds. — Proc. Roy. Soc. Lond. B: Biol. Sci. 278: 1019-1024.

Brommer, J.E. & Kluen, E. (2012). Exploring the genetics of nestling personality traits in a wild passerine bird: testing the phenotypic gambit. — Ecol. Evol. 2: 3032-3044.

Carere, C. & van Oers, K. (2004). Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. — Physiol. Behav. 82: 905-912.

Christensen, R.H.B. (2018). Ordinal: regression models for ordinal data. — R package version 2018.8-25, R Foundation for Statistical Computing, Vienna, available online at https://CRAN.R-project.org/package=ordinal/.

Class, B., Kluen, E. & Brommer, J.E. (2014). Evolutionary quantitative genetics of behavioral responses to handling in a wild passerine. — Ecol. Evol. 4: 427-440.

Class, B. & Brommer, J.E. (2015). A strong genetic correlation underlying a behavioural syndrome disappears during development because of genotype-age interactions. — Proc. Roy. Soc. Lond. B: Biol. Sci. 282: 20142777.

Class, B. & Brommer, J.E. (2016). Senescence of personality in a wild bird. — Behav. Ecol. Sociobiol. 70: 733-744.

David, M., Auclair, Y., Dechaume-Moncharmont, F.X. & Cézilly, F. (2012). Handling stress does not reflect personality in female zebra finches (*Taeniopygia guttata*). — J. Comp. Psychol. 126: 10-14.

Davies, N.B. (2000). Cuckoos, cowbirds and other cheats. — T & AD Poyser, London.

Dingemanse, N.J., Both, C., Drent, P.J., van Oers, K. & van Noordwijk, A.J. (2002). Repeatability and heritability of exploratory behavior in great tits from the wild. — Anim. Behav. 64: 929-937.

Dingemanse, N.J., Both, C., Drent, P.J. & Tinbergen, J.M. (2004). Fitness consequences of avian personalities in a fluctuating environment. — Proc. Roy. Soc Lond. B: Biol. Sci. 271: 847-852.

Dingemanse, N.J., Wright, J., Kazem, A.J.N., Thomas, D., Hickling, R. & Dawnay, N. (2007). Behavioral syndromes differ predictably between 12 populations of three-spined stickleback. — J. Anim. Ecol. 76: 1128-1138.

Dingemanse, N.J., Kazem, A.J.N., Réale, D. & Wright, J. (2010). Behavioral reaction norms: animal personality meets individual plasticity. — Trends. Ecol. Evol. 25: 81-89.

Eising, C.M., Muller, W. & Groothuis, T.G.G. (2006). Avian mothers create different phenotypes by hormone deposition in their eggs. — Biol. Lett. 2: 20-22.

Favati, A., Zidar, J., Thorpe, H., Jensen, P. & Løvlie, H. (2016). The ontogeny of personality traits in the red junglefowl, *Gallus gallus*. — Behav. Ecol. 27: 484-493.

Forstmeier, W. & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. — Behav. Ecol. Sociobiol. 65: 47-55.

Fresneau, N., Kluen, E. & Brommer, J.E. (2014). A sex-specific behavioral syndrome in a wild passerine. — Behav. Ecol. 25: 359-367.

Fucikova, E., Drent, P.J., Smits, N. & van Oers, K. (2009). Handling stress as a measurement of personality in great tit nestlings (*Parus major*). — Ethology 115: 366-374.

Glutz von Blotzheim, U.N. & Bauer, K.M. (1980). Handbuch der Vögel Mitteleuropas, Bd 9. Columbiformes – Piciformes. — Akademische Verlagsgesellschaft, Wiesbaden.

Grafen, A. & Hails, R. (2002). Modern statistics for the life sciences. — Oxford University Press, Oxford.

Grim, T. (2006). Cuckoo growth performance in parasitized and unused hosts: not only host size matters. — Behav. Ecol. Sociobiol. 60: 716-723.

Grim, T. (2007a). Equal rights for chick brood parasites. — Ann. Zool. Fenn. 44: 1-7.

Grim, T. (2007b). Experimental evidence for chick discrimination without recognition in a brood parasite host. — Proc. Roy. Soc. Lond. B: Biol. Sci. 274: 373-381.

Grim, T. & Honza, M. (2001). Does supernormal stimulus influence parental behaviour of the cuckoo's host? — Behav. Ecol. Sociobiol. 49: 322-329.

Grim, T., Samaš, P. & Hauber, M.E. (2014a). The repeatability of avian egg ejection behaviors across different temporal scales, breeding stages, female ages and experiences. — Behav. Ecol. Sociobiol. 68: 749-759.

Grim, T., Samaš, P., Moskát, C., Kleven, O., Honza, M., Moksnes, A., Røskaft, E. & Stokke, B.G. (2011). Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? — J. Anim. Ecol. 80: 508-518.

Grim, T., Samaš, P., Procházka, P. & Rutila, J. (2014b). Are tits really unsuitable hosts for the common cuckoo? — Ornis Fenn. 91: 166-177.

Grim, T. & Samaš, P. (2016). Growth performance of nestling cuckoos *Cuculus canorus* in cavity nesting hosts. — Acta Ornithol. 51: 175-188.

Grim, T., Tyller, Z. & Samaš, P. (2017). Unusual diet of brood parasite nestlings and its fitness consequences. — Auk 134: 732-750.

Groothuis, T.G.G. & Carere, C. (2005). Avian personalities: characterization and epigenesis. — Neurosci. Biobehav. Rev. 29: 137-150.

Groothuis, T.G.G., Muller, W., von Engelhardt, N., Carere, C. & Eising, C.M. (2005). Maternal hormones as a tool to adjust offspring phenotype in avian species. — Neurosci. Biobehav. Rev. 29: 329-352.

Groothuis, T.G.G., Carere, C., Lipar, J., Drent, P.J. & Schwabl, H. (2008). Selection on personality in a songbird affects maternal hormone levels tuned to its effect on timing of reproduction. — Biol. Lett. 4: 465-467.

Guigueno, M.F. & Sealy, S.G. (2011). Aggression towards egg-removing cowbird elicits clutch abandonment in parasitized yellow warblers, *Dendroica petechia*. — Anim. Behav. 81: 211-218.

Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models. The MCMCglmm R package. — J. Stat. Softw. 33: 1-22.

Hanley, D., Samaš, P., Heryán, J., Hauber, M.E. & Grim, T. (2015). Now you see it, now you don't: flushing hosts prior to experimentation can predict their responses to brood parasitism. — Sci. Rep. 5: 9060.

Hargitai, R., Costantini, D., Moskát, C., Bán, M., Muriel, J. & Hauber, M.E. (2012). Variation in plasma oxidative status and testosterone level in relation to egg-eviction effort and age of brood-parasitic common cuckoo nestlings. — Condor 114: 782-791.

Hauber, M.E. & Ramsey, C.K. (2003). Honesty in host-parasite communication signals: the case for begging by fledgling brown-headed cowbirds *Molothrus ater*. — J. Avian Biol. 34: 339-344.

Hauber, M.E., Samaš, P., Anderson, M.G., Rutila, J., Low, J., Cassey, P. & Grim, T. (2014). Life-history theory predicts host behavioural responses to experimental brood parasitism. — Ethol. Ecol. Evol. 26: 349-364.

Hollander, F.A., van Overveld, T., Tokka, I. & Matthysen, E. (2008). Personality and nest defence in the great tit (*Parus major*). — Ethology 114: 405-412.

Hoover, J.P. & Robinson, S.K. (2007). Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. — Proc. Natl. Acad. Sci. USA 104: 4479-4483.

Igic, B., Zarate, E., Sewell, M.A., Moskát, C., Cassey, P., Rutila, J., Grim, T., Shawkey, M.D. & Hauber, M.E. (2015). A comparison of egg yolk lipid constituents between parasitic common cuckoos and their hosts. — Auk 132: 817-825.

Karlíková, Z., Kejzlarová, T. & Šálek, M. (2018). Breath rate patterns in precocial northern lapwing (*Vanellus vanellus*) chicks in the wild. — J. Ornithol. 159: 555-563.

Kleven, O., Moksnes, A., Røskaft, E. & Honza, M. (1999). Host species affects the growth rate of cuckoo (*Cuculus canorus*) chicks. — Behav. Ecol. Sociobiol. 47: 41-46.

Krams, I.A., Vrublevska, J., Sepp, T., Abolins-Abols, M., Rantala, M.J., Mierauskas, P. & Krama, T. (2014). Sex-specific associations between nest defence, exploration and breathing rate in breeding pied flycatchers. — Ethology 120: 492-501.

Langenhof, M.R. & Komdeur, J. (2018). Why and how the early-life environment affects development of coping behaviours. — Behav. Ecol. Sociobiol. 72: 34.

Lesnoff, M. & Lancelot, R. (2012). Analysis of overdispersed data. — R package version 1.3, available online at http://cran.r-project.org/package=aod.

Li, D., Zhang, Z., Grim, T., Liang, W. & Stokke, B.G. (2016). Explaining variation in brood parasitism rates between potential host species with similar habitat requirements. — Evol. Ecol. 30: 905-923.

Martín-Gálvez, D., Soler, M., Soler, J.J., Martín-Vivaldi, M. & Palomino, J.J. (2005). Food acquisition by common cuckoo chicks in rufous bush robin nests and the advantage of eviction behaviour. — Anim. Behav. 70: 1313-1321.

McCowan, L.S.C. & Griffith, S.C. (2014). Nestling activity levels during begging behavior predicts activity level and body mass in adulthood. — PeerJ 2: e566.

Mikulica, O., Grim, T., Schulze-Hagen, K. & Stokke, B.G. (2017). The cuckoo: the uninvited guest. — Wild Nature Press, Plymouth.

Moksnes, A., Røskaft, E., Hagen, L.G., Honza, M., Mørk, C. & Olsen, P.H. (2000). Common cuckoo *Cuculus canorus* and host behaviour at reed warbler *Acrocephalus scirpaceus* nests. — Ibis 142: 247-258.

Nakagawa, S. & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. — Biol. Rev. 85: 935-956.

Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. — Methods Ecol. Evol. 4: 133-142.

Palme, R., Rettenbacher, S., Touma, C., El-Bahr, S.M. & Möstl, E. (2005). Stress hormones in mammals and birds: comparative aspects regarding metabolism, excretion, and noninvasive measurement in fecal samples. — Ann. N.Y. Acad. Sci. 1040: 162-171.

Polverino, G., Cigliano, C., Nakayama, S. & Mehner, T. (2016a). Emergence and development of personality over the ontogeny of fish in absence of environmental stress factors. — Behav. Ecol. Sociobiol. 70: 2027-2037.

Polverino, G., Ruberto, T., Staaks, G. & Mehner, T. (2016b). Tank size alters mean behaviours and individual rank orders in personality traits of fish depending on their life stage. — Anim. Behav. 115: 127-135.

Požgayová, M., Procházka, P. & Honza, M. (2009). Sex-specific defence behaviour against brood parasitism in a host with female-only incubation. — Behav. Proc. 81: 34-38.

Požgayová, M., Piálková, R., Honza, M. & Procházka, P. (2018). Sex-specific nestling growth in an obligate brood parasite: common cuckoo males grow larger than females. — Auk 135: 1033-1042.

Prokop, P., Trnka, R. & Trnka, A. (2009). First videotaped infanticide in the common pochard *Aythya ferina*. — Biologia 64: 1016-1017.

Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. — Phil. Trans. Roy. Soc. Lond. B: Biol. Sci. 365: 4051-4063.

Revelle, W. (2018). psych: procedures for personality and psychological research. — Northwestern University, Evanston, IL, available online at https://CRAN.R-project.org/package=psych.

Robertson, R.J. & Norman, R.F. (1977). The function and evolution of aggressive host behavior towards the brown-headed cowbird (*Molothrus ater*). — Can. J. Zool. 55: 508-518.

Rothstein, S.I. (1990). A model system for coevolution: avian brood parasitism. — Annu. Rev. Ecol. Syst. 21: 481-508.

Ruotsalainen, S. (2017). Univariate and multivariate statistical tests in genetic association studies. — Master's thesis, University of Helsinki, Helsinki.

Samaš, P., Hauber, M.E., Cassey, P. & Grim, T. (2011). Repeatability of foreign egg rejection: testing the assumptions of co-evolutionary theory. — Ethology 117: 606-619.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. — Methods Ecol. Evol. 1: 103-113.

Schuett, W., Tregenza, T. & Dall, S.R.X. (2010). Sexual selection and animal personality. — Biol. Rev. 85: 217-246.

Sih, A., Bell, A.M. & Johnson, J.C. (2004). Behavioral syndromes: an ecological and evolutionary overview. — Trends. Ecol. Evol. 19: 372-378.

Smith, B.R. & Blumstein, D.T. (2008). Fitness consequences of personality: a meta-analysis. — Behav. Ecol. 19: 448-455.

Soler, M., Soler, J.J., Martinez, J.G. & Møller, A.P. (1995). Magpie host manipulation by great spotted cuckoos: evidence for an avian mafia? — Evolution 49: 770-775.

Soler, M. (ed.) (2017). Avian brood parasitism: behaviour, ecology, evolution and coevolution. — Springer, New York, NY.

Soma, K.K. (2006). Testosterone and aggression: Berthold, birds and beyond. — J. Neuroendocrinol. 18: 543-551.

Stamps, J.A. & Groothuis, T.G.G. (2010a). Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. — Phil. Trans. Roy. Soc. Lond. B: Biol. Sci. 365: 4029-4041.

Stamps, J.A. & Groothuis, T.G.G. (2010b). Ontogeny of animal personality: relevance, concepts and perspectives. — Biol. Rev. 85: 301-325.

Torné-Noguera, A., Pagani-Núñez, E. & Senar, J.C. (2014). Great tit (*Parus major*) breath rate in response to handling stress: urban and forest birds differ. — J. Ornithol. 155: 315-318.

Török, J., Moskát, C., Michl, G. & Péczely, P. (2004). Common cuckoos (*Cuculus canorus*) lay eggs with larger yolk but not more testosterone than their great reed warbler (*Acrocephalus arundinaceus*) hosts. — Ethol. Ecol. Evol. 16: 271-277.

Trnka, A. (1995). Dietary habits of the great reed warbler (*Acrocephalus arundinaceus*) young. — Biologia 50: 507-512.

Trnka, A., Batáry, P. & Prokop, P. (2009). Interacting effects of vegetation structure and breeding patterns on the survival of great reed warbler *Acrocephalus arundinaceus* nests. — Ardea 97: 109-116.

Trnka, A., Prokop, P. & Batáry, P. (2010). Infanticide or interference: does the great reed warbler selectively destroy eggs? — Ann. Zool. Fenn. 47: 272-277.

Trnka, A. & Prokop, P. (2011). Polygynous great reed warblers *Acrocephalus arundinaceus* suffer more cuckoo *Cuculus canorus* parasitism than monogamous pairs. — J. Avian Biol. 42: 192-195.

Trnka, A., Požgayová, M., Samaš, P. & Honza, M. (2013). Repeatability of host female and male aggression towards a brood parasite. — Ethology 119: 907-917.

Trnka, A. & Grim, T. (2014). Testing for correlation between behaviours in a cuckoo host: why do host defences not covary? — Anim. Behav. 92: 185-193.

Trnka, A., Požgayová, M., Procházka, P., Čapek, M. & Honza, M. (2016). Chemical defence in avian brood parasites: production and function of repulsive secretions in common cuckoo chicks. — J. Avian Biol. 47: 288-293.

Trnka, A., Samaš, P. & Grim, T. (2018). Stability of a behavioural syndrome vs. plasticity in individual behaviours over the breeding cycle: ultimate and proximate explanations. — Behav. Proc. 153: 100-106.

Tyller, Z., Kysučan, M. & Grim, T. (2018). Postfledging behavior of the common cuckoo (*Cuculus canorus*) attended by the chaffinch (*Fringilla coelebs*): a comprehensive approach to study the least known stage of brood parasite-host coevolution. — Wilson. J. Ornithol. 130: 536-542.

van Oers, K., de Jong, G., Van Noordwijk, A.J., Kempenaers, B. & Drent, P.J. (2005). Contribution of genetics to the study of animal personalities: a review of case studies. — Behaviour 142: 1191-1212.

van Oers, K. & Carere, C. (2007). Long-term effects of repeated handling and bleeding in wild caught great tits *Parus major*. — J. Ornithol. 148: S185-S190.

van Oers, K., Kohn, G.M., Hinde, C.A. & Naguib, M. (2015). Parental food provisioning is related to nestling stress response in wild great tit nestlings: implications for the development of personality. — Front. Zool. 12: S10.

Verbeek, M.E.M., Boon, A. & Drent, P.J. (1996). Exploration, aggressive behavior and dominance in pair-wise confrontations of juvenile male great tits. — Behaviour 133: 945-963.

von Engelhardt, N., Carere, C., Dijkstra, C. & Groothuis, T.G.G. (2006). Sex specific effects of yolk testosterone on offspring survival, begging and growth in the zebra finch. — Proc. Roy. Soc. Lond. B: Biol. Sci. 273: 65-70.

Willemoes, M., Strandberg, R., Klaassen, R.H., Tøttrup, A.P., Vardanis, Y., Howey, P.W., Thorup, K., Wikelski, M. & Alerstam, T. (2014). Narrow-front loop migration in a population of the common cuckoo *Cuculus canorus*, as revealed by satellite telemetry. — PLoS ONE 9: e83515.

Wingfield, J.C., Ball, G.F., Dufty, A.M., Hegner, R.E. & Ramenofsky, M. (1987). Testosterone and aggression in birds. — Am. Sci. 75: 602-608.

Wuerz, Z. & Krüger, O. (2015). Personality over ontogeny in zebra finches: long-term repeatable traits but unstable behavioural syndromes. — Front. Zool. 12: S9.

Wyllie, I. (1981). The cuckoo. — Batsford, London.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. — Methods Ecol. Evol. 1: 3-14.