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The hissing behaviour of great tit (*Parus major*) females reflects behavioural phenotype and breeding success in a wild population

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Press

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I Krams, I., Vrublevska, J., **Koosa, K.**, Krama, T., Mierauskas, P., Rantala, M. J., Tilgar, V. 2014. Hissing calls improve survival in incubating female great tits (*Parus major*). Acta Ethologica 17, 83–88.

II **Koosa, K.**, Tilgar, V. 2016. Is hissing behaviour of incubating great tits related to reproductive investment in the wild? 2016. Acta Ethologica 19, 173–180.

III Tilgar, V., **Koosa, K.** 2019. Hissing females of great tits (*Parus major*) have lower breeding success than non-hissing individuals. Ethology 125, 949–956.

IV Timm, K., **Koosa, K.**, Tilgar, V. 2019. The serotonin transporter gene could play a role in anti-predator behaviour in a forest passerine. Journal of Ethology 37, 221–227.

K. Hein and K. Koosa are the same person, name Koosa changed into Hein in 2019. Published papers are reproduced with the permission of the publishers.

My contribution to the papers was as follows ('*' denotes a contribution equal to 0.33, '**' denotes a contribution of 0.66, '***' denotes contribution of 1.00):

	I	II	III	IV
Original idea		***	***	*
Study design		**	**	*
Data collection	*	**	**	**
Data analysis	*	**	**	*
Manuscript preparation	*	***	**	*

1. INTRODUCTION

The causes and the consequences of individual behavioural differences have become a great interest of species' ecology and evolution (Sih *et al.* 2004, Réale *et al.* 2007, Schuett *et al.* 2010, Wolf and Weissing 2012) as well as conservation biology (McDougall *et al.* 2006, Archard and Braitwhite 2010). Individual differences from the optimal behaviour of a species are no longer considered as 'noise' but as different individual behavioural strategies (Bell *et al.* 2009, Réale *et al.* 2010). It is now commonly understood that individual animals, as with humans, have stable behavioural differences between individuals called personalities that stay consistent over time and in changing environments (Gosling 2008, Turner *et al.* 2017). Animals make decisions derived from their personality that affect individual fitness, and thus personality traits are subjected to natural selection. As natural selection maintains diversity in animal personalities, one of the greatest interests is in growing our understanding of the importance of the personality in animal ecology, and to determine the underlying mechanisms causing such behavioural variety.

Researchers are still divided about the effectiveness of the various practises employed in measuring and defining animal personality (Roche *et al.* 2016). This is because personality in animals is difficult to evaluate. Following Réale *et al.* (2007), a behavioural trait may be attributed to animal personality if it has been shown to be variable between individuals of the same population, repeatable across time and contexts, and, if possible, heritable from parents to offspring. Koolhaas *et al.* (1999) described so-called coping styles in artificially selected mice, where the term 'proactive' was assigned to more aggressive, risk-taking, routine-forming individuals, and the term 'reactive' to shy, less risk-prone, yet more flexible individuals, thus linking the behavioural phenotype to physiological characteristics. To date, it is the most common practice to categorise animal personalities along a two-dimensional axis – the proactive-reactive, or slow-fast continuum (e.g., exploration, Both *et al.* 2005, dispersal, Carter *et al.* 2013). However, behavioural traits are often correlated within or across contexts, forming behavioural syndromes as defined by Sih *et al.* 2004. For example, boldness is often correlated with aggressiveness, in that otherwise bolder individuals may also be more aggressive towards conspecifics, or predators (Grinsted and Bacon 2014). All this underlines the need to carefully consider what traits are suitable when interpreting animal personality. Also, it is necessary to study behavioural responses across contexts and incorporate both behavioural and physiological aspects when addressing fitness consequences.

An important aspect when interpreting behavioural tests is that behaviour may vary whether it is observed in the wild, on free-living animals, or in captivity. The advantages of studying behaviour under laboratory conditions are well-known: several factors influencing behaviour can be eliminated (predators, conspecifics, even condition) or enabled (unlimited access to food and water). On the other hand, behavioural traits measured under standardised conditions (e.g., the behavioural response of individuals captured from the wild, measured using tests conducted under laboratory conditions) may not be of ecological importance in the wild (Nussey *et al.* 2007, Arvidsson *et al.* 2017), or even worse, may be stress-induced (Vincze *et al.* 2016). It has been even shown that individuals taken from the wild for laboratory-testing may be pre-selected based on their tendency to get trapped (e.g., collared flycatchers, *Ficedula albicollis*, Garamszegi *et al.* 2009), resulting in false estimates of behavioural variability in the measured traits. Furthermore, in a large meta-analysis, Bell *et al.* (2009) concluded that repeatability measures tend to be higher when behavioural traits have been measured in the wild. Naturally occurring behaviour is most likely under natural selection, that is, behavioural differences exist due to different effect on life-history.

Numerous case studies across taxa clearly demonstrate that consistent individual differences in behaviour, measured in the field, correlate to various life-history traits. For example, in a group forming spider species, naturally occurring groups that have both aggressive and docile phenotypes lead to higher overall fitness (Grinsted and Bacon 2014). In lizards, Cote *et al.* (2008) demonstrated that juvenile survival was related to individual social tolerance in relation to population density. In birds, Dingemanse *et al.* (2004) linked survival of different behavioural phenotypes to food availability. In mammals, Boon *et al.* 2007 demonstrated for squirrels that offspring fitness was affected by the female's activity and aggressiveness. Hence, in the wild, any behavioural aspect commonly attributed to a species' ecology, that exhibits phenotypic variability between individuals and repeatability within individual, should be of interest for further investigation as a personality trait, and its subsequent relevance to fitness.

Risk-related behaviours, such as anti-predator behaviour, are one of the most important traits affecting individual fitness (Caro 2005). Prey-predator interactions through direct threat, as well as offspring fitness through the parents' ability to defend both themselves and the offspring influence individual fitness. It is commonly known that individual animals may react differently towards predators or risky situations. Bize *et al.* (2012) managed to reveal that anti-predator behaviour was individually repeatable and heritable (measured as flight or freeze behaviour in the Alpine swift, *Apus melba*). As this theoretical framework developed, David and Dall (2016) suggested that pronounced anti-predator responses maintain a fast 'pace-of-life' and high productivity, meaning that behavioural responses might be related to reproductive decisions. For example, aggressive, bold, and exploratory behavioural types could therefore be related to high reproductive values (e.g., number of offspring). At the same time, behaviour may be influenced by several extrinsic factors, such as a predator's propensity or mobbing group size (Krams *et al.* 2010, Tilgar and Moks 2015). Parental investment theory is another important aspect to be considered, suggesting that anti-predator behaviour is strongly related to the reproductive value of the offspring (Tilgar and Kikas 2009). In short, it must be carefully considered at what point, or to what extent exactly anti-predator behaviour reflects personality.

A common way to experimentally investigate anti-predator strategies in the wild is to measure predator avoidance, e.g., flight initiation distance in birds

(Møller and Erritzøe 2013). A promising line of research could be to determine if predator-avoidance also indicated personality. However, not all species are that easy to get close to, for example, when studying small passerine species inhabiting large forest areas. In such cases it is possible to study behavioural differences in anti-predator strategies during breeding season, when nests can be located, and parent birds are more easily identified. In cavity-nesting birds, providing artificial nesting sites (nest-boxes) may help to gather efficient sample size. In several bird species, a form of anti-predator behaviour – the hissing behaviour – is often considered as an act of nest defence, as it has been related to incubating females (Sibley 1955). However, in tits, for example, the hissing behaviour is relevant in both sexes (Sibley 1955; personal observations). It has been reported in some bird species that even the offspring may elicit hissing sounds towards a potential predator (e.g., barn owls, van der Brink 2012). Furthermore, such behaviour has been described in various taxa unrelated to breeding behaviour (e.g., bumblebees – Kirchner and Röschard 1999, lizards – Labra *et al.* 2007). Hissing is a behavioural trait that is relatively easy to measure in the wild, thus making it a potentially useful trait when evaluating the personality type of the bird species, or perhaps even species of other taxa. In Table 1, I give a brief overview of methods that have been used to measure hissing behaviour, focusing on whether there is any information regarding its relation to individual personality. Table 1 also illustrates the necessity to apply repeatable methodology for comparable studies across various experiments in the field.

The great tit (*Parus major*) is a well-studied model species, making it a valuable candidate to further develop the theoretical framework for studying animal personality (Groothuis and Carere 2005). Great tits are short-lived, cavity-nesting birds that readily occupy human provided artificial nest-sites (Mänd *et al.* 2005) and are known to cope well with handling. In recent years, great tits have been subjected to multiple study designs that have contributed to personality studies both in captivity and in the wild (Drent *et al.* 2003, Dingemanse *et al.* 2004, Both *et al.* 2005, van Overveld and Matthysen 2010, Cole and Quinn 2014). The genome-related studies of the great tit have further advanced personality research (van Oers *et al.* 2004, Ryahi *et al.* 2015, Timm *et al.* 2018). The great tit presumably performs hissing display as an act of defence when suddenly confronted with a predator (Sibley 1955), for example, when a bird is inside a cavity and a potential predator blocks its escape. In this situation both males and females are known to emit hissing sounds, accompanied by banging the wings and false attacks targeted at the intruder (personal obs.). It is commonly thought that such behaviour may allow the defending bird a possibility of escape as the intruder may be intimidated by the hissing sounds (Zub *et al.* 2017). However, escaping shortly after hissing is not a common occurrence, at least among incubating female great tits (personal obs.). Whilst hissing should be considered as a beneficial behaviour in predator-related contexts (Zub *et al.* 2017), a considerable number of individuals do not hiss when confronted with a threatening situation (Sibley 1955, personal obs.).

Table 1. Literature overview of recent papers reporting to have measured hissing behaviour in the tit family (*Paridae*). A few selected indices illustrate what and how have been measured, and whether they found any other relevant information about hissing behaviour

Author(s), year	**Region**	**What was measured?**	**Significant repeatability, or percentage of hissing birds**	**How was hissing provoked?**	**Associations with other traits, or genes**
Dutour *et al*. 2020	France	Hissing (yes/no)	–	With a stick	Hissing had a deterring effect on a predator
Grunst *et al*. 2018	Belgium	Number of hisses per 60 seconds	R=0.638	Woodpecker decoy	Exploration (varied); metal pollution (not related)
Møller *et al*. 2021	Denmark, China	Reaction type (including hissing display)	Denmark: 27% of birds hiss, R=0.27; China: 71% of birds hiss	Nest-box lid opened	Hissing more common in areas with more snakes
Riyahi *et al*. 2022	Spain	Number of hisses per 15 seconds	44% of birds hiss	Mouse model	*SERT* gene (SNP290) was related to hissing
Thys *et al*. 2019	Belgium	Number of hisses per 60 seconds	R=0.79 (incubation), R=0.81 (overall)	Woodpecker decoy	Plasticity (individual, and population level)
Thys *et al*. 2021	Belgium	Number of hisses per 60 seconds	–	Woodpecker decoy	Aggressiveness (not associated with hissing)
Zhang *et al*. 2020	China	Hissing (yes/no)	5 tit species, range=17.6–82.3%	Nest-box lid opened	Predation risk (did not differ between groups)
Zub *et al*. 2017	Poland	Hissing (yes/no)	–	Not clear (recording)	Hissing had a deterring effect on a predator

So why do some birds remain silent and more importantly, if such behaviour might negatively affect survival, how do these birds benefit? The exact mechanisms behind adopting such counterintuitive, naturally occurring behaviour remain the subject of future research. The aim of this thesis was to characterise hissing behaviour as a personality trait of free-living female great tits. More specifically, I wanted to examine whether these behavioural characteristics are attributable to animal personality as defined by Réale *et al.* (2007) – is hissing variable across the same population over seasons, do individuals behave consistently in time, and is such behavioural variety detectable by genetic differences. Within these aims I will associate hissing response types (so-called hissing and non-hissing birds) with life-history traits (survival, reproductive investment, breeding success) in their natural habitat, and examine individual differences in genetic variability within these different behavioural groups.

The interpretation of behaviour of free-living animals is complicated owing to several uncontrollable environmental factors, some of which are also addressed in this study. To minimise the behavioural effect of the partner of the incubating female and to avoid the potential distress calls of the nestlings, the experiment was carried out during the early breeding (incubation) stage. This targeted the time period where the behaviour of the female should be determined by her own decision-making. In addition, anti-predator behaviour has been shown to be dependent on the value of the brood (for instance, number of eggs or age of the nestlings). The current study hopefully may elucidate whether hissing is more of a self-defence rather than nest-defence by considering clutch size as a covariate in all models. Moreover, it is possible that anti-predator behaviour may be influenced by the relative abundance of potential (nest) predators (Lima 2009), therefore depredated nests during the study period were considered as an indicator of predation probability (or, predator abundance). I hope to give evidence that a specific, naturally occurring behavioural trait – in this case, hissing – may be of great importance when applying behavioural tests in the field.

I hypothesized as follows:

1. Hissing or non-hissing is a consistent behavioural trait along the slow-fast axis, and therefore individually repeatable both within season and across seasons.
2. The propensity to hiss can be related to the reproductive investment and the expected lifespan.
3. Hissing may be influenced by environmental conditions such as predator abundance and population density.
4. Hissing and non-hissing birds differ genetically: hissing behaviour is associated with polymorphism in two candidate genes, the serotonin transporter gene (*SERT*) and the dopamine receptor gene D4 (*DRD4*).

2. METHODS

2.1. Study site and subject

Data were collected in the forests of southwest Estonia at Kilingi-Nõmme study site (58°7′N, 25°5′E) between 2011 and 2014. The study area of over 1000 nest-boxes is about 50 km^2 (Figure 1). It is largely covered by a mosaic of deciduous and coniferous forest. The conifer woodlands are mostly managed pine (*Pinus sylvestris*) forests on nutrient-poor sandy or peaty soils. Deciduous woodlands occur mainly as isolated patches between cultivated fields or as belts along stream valleys. Growing on fertile soils and having a rich deciduous understorey, the dominant tree species are grey alder (*Alnus incana*) and silver birch (*Betula pendula*).

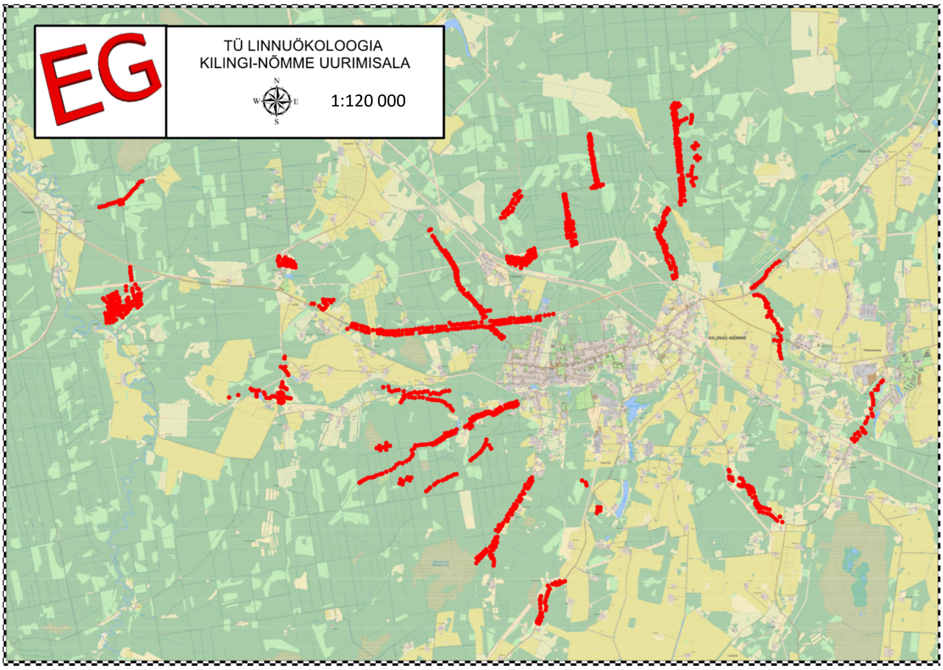

Figure 1. Study area of the rural great tit population at Kilingi-Nõmme (by Jaanis Lodjak). Nest-boxes, assembled as transects, are marked in red. Green areas represent forests, yellow areas refer to arable land. The human population in the town is 1716 (Statistics Estonia, 2017).

The great tit is a small, short-lived, cavity-breeding passerine bird, that is widespread throughout the Palearctic region. Only the female builds the nest and incubates the eggs (Perrins 1979). Their natural nest predators include the sparrowhawk (*Accipiter nisus*), the Eurasian pygmy owl (*Glaucidium passerinum*), the great spotted woodpecker (*Dendrocopos major*), the pine marten (*Martes

martes) and the red squirrel (*Sciurus vulgaris*). The latter three predators threaten eggs and nestlings in particular but also the incubating females.

The great tits in the study population bred in nest-boxes mounted on tree trunks at a height of 1.5–1.8 m. More details about the nest-box arrangement are described in Paper **II**. Nests were checked throughout the nesting period to obtain data on the onset of egg-laying (hereafter called ‘lay-date’), clutch size, start of incubation, and the number of fledglings (15-day-old). Adults were caught using nest-box traps and were measured and ringed during the second half of the nestling period (days 7–15 post-hatch). Fledglings and adults were weighed using a Pesola spring balance to a precision of 0.1 g, and tarsus length was measured to the nearest 0.1 mm with a digital calliper. Recapture rates of the ringed females were determined in 2012–2015. Blood samples for genotyping were collected in 2012. Blood samples (~ 70 μl) were taken from a brachial vein with a sterile lancet and collected in a heparinized capillary tube (immediately stored at + 4 °C, afterwards centrifuged to separate cells from plasma for further hormone analysis, and finally stored at −80 °C until required for DNA analysis).

2.2. Behavioural experiment

Great tits may breed twice per season; my study was carried out during the first breeding attempt (during April and May in the study area). The anti-predator behaviour of females was tested in the first half of the incubation period. Day 0 of incubation started when a female laid her last egg. The initial trial was conducted around 5–7 days after females started incubating (with a few exceptions).

A stuffed great spotted woodpecker was presented to incubating females through the nest-hole (only the head of the woodpecker was visible to the incubating bird) and it was recorded whether birds gave hissing calls in reply. If the female reacted, then distinct hissing sounds were heard coming from inside the nest-box, sometimes accompanied by the sound of the banging of wings against the walls of the nest-box. If the bird did not react, the lid of the nest-box was removed to confirm the presence of the female.

The aim was to measure the hissing behaviour during a relatively short time interval as females usually reply quickly to disturbance and the startle effect against a predator may work best in the first few seconds. Initially the response was measured for up to 30 seconds (I). As most of the responding females hissed during the first 5 seconds (72% of responding birds in 2011), from then on, the response was measured for up to 5 seconds (II, III, IV). Based on each female’s reaction towards the woodpecker during this 5-second trial, birds were divided into hissing (responded) and non-hissing (did not respond) groups (hereafter called ‘response type’). To assess the trait repeatability, in 2011 and 2012 a number of birds (N = 69) were given a repeat trial 3–5 days later. In addition, in 2011 and 2013, hissing delay was measured as a continuous parameter (latency to start hissing after the woodpecker had been presented, 1–5 seconds). Note that in 2011 the delay value varied between 1–29 seconds, however, as it quickly became clear that the majority of the hissing birds give a hissing display within the first few seconds, the time interval for behavioural testing was reduced to 5 seconds from then on (see also Paper II). Hence, the minimum delay value was always considered to be 1 second, and the maximum delay was 5 seconds.

2.3. Genotyping

Altogether, 62 females were tested for hissing response and later trapped and genotyped in 2012 (genotyping details are fully described in Paper **IV**). Of these 62 birds, 32 hissed and 30 did not hiss. In the *SERT* gene, two loci were studied that are known to affect bird behaviour (promoter region and exon 1) (Mueller *et al.* 2013, Riyahi *et al.* 2015). For the *DRD4* gene, polymorphisms were visually examined of aligned sequences using the ChromasPro 1.7.6 programme.

2.4. Statistical analysis

All analyses were performed using R. The repeatabilities of response latency to in hissing calls and the number of hissing calls given were calculated across two trials using Lessells and Boag's (1987) method. General linear mixed model (GLM) and general linearized models with binomial link (GLZ) were used for the analyses correlating hissing type and delay to reproductive characteristics and environmental factors, and to *DRD4* and *SERT* polymorphisms (SNPs). Chi-square tests were also employed for testing the Hardy–Weinberg equilibrium in genotype frequencies in the population (Rodriguez *et al.* 2009). To cover allelic and genotypic effects, a general genetic model was used in the analysis, including three distinct genotype categories. As five SNPs were included, Bonferroni correction for the number of independent SNPs was also employed.

2.5. Ethical statement

Data collecting (ringing, blood sampling, behavioural experiments) complied with the laws of Estonia and were approved by the Animal Procedures Committee of the Estonian Ministry of Agriculture and by the Estonian Department of Environment. The conditions stated in the licences were followed during the study. No nests were deserted, and no individuals were killed unless due to natural causes, e.g., predation.

3. RESULTS

3.1. The variability and repeatability of hissing behaviour (I, II, III)

Over the 4-year study period (2011–2014), 187 out of 300 females (62%) gave hissing calls when exposed to the woodpecker dummy, while 113 (38%) individuals did not respond to the same stimulus (**III**). The proportion of hissing females was relatively consistent across years (range = 55–68%) (**III**).

The repeatability of hissing behaviour was measured during a 3-year study period in 2011–2013 (2011: response type, hissing delay; 2012 response type; 2013 hissing delay). Repeatability of hissing or non-hissing behavioural type when measured 3–5 days later was highly repeatable (**II**). Individuals among hissing females also showed significant repeatability in the latency to start hissing (hissing delay) and the number of hisses given between repeated trials (**I**).

Additionally, 15 individuals that were tested for hissing behaviour were recaptured in a subsequent year during the period 2011–2015. The response type of those 15 individuals was repeatable across seasons (12 out of 15 recaptured females did not change their response; **III**).

3.2. Female quality, reproductive investment, and recapture probability in comparison to the hissing and non-hissing birds (II, III)

Data on female body mass were associated with reproductive characteristics and the hissing behaviour. Hissing did not directly relate to female body mass, the start of egg-laying or clutch size (**II**). However, the heavier females among non-hissing birds laid earlier in the season, whereas no such pattern was found among hissing birds. The hissing delay among the hissing females was non-linearly linked to lay-date in the 5 second trial (early breeders responded more rapidly) (**II**).

The number of fledglings among successful nests was close to significantly larger for non-hissing birds (**III**). Reproductive success (the proportion of eggs producing fledglings) was remarkably higher for non-hissing females compared with the hissing group (89% vs. 82%). Furthermore, hatching success between hissing types did not differ (93% in both groups) while fledging success from neonates to fledglings was significantly higher for non-hissing birds (96% vs. 88%) and was higher for deciduous forests when compared to coniferous forests (94% vs. 89%). The probability of successful breeding (nest fails/successes) did not relate to a female's hissing response type. In the incubation or nestling stage, 25 of 145 nests failed in the hissing group and 11 out of 84 in the non-hissing group (**III**) over 4 years. The mean fledgling mass per brood did not differ between groups. No interaction between year (fixed factor) and hissing type was found for breeding parameters in any models (**III**).

Hissing females may have had increased life expectancy in comparison with non-hissing birds (**unpublished data**). The recapture rate was higher for responding compared with non-responding birds ($\chi^2 = 5.67$, df = 1, $P = 0.017$, Figure 2) while this trait was not affected by other predictors in the model (habitat: $\chi^2 = 1.78$, df = 1, $P = 0.18$; female mass: $\chi^2 = 0.30$, df = 1, $P = 0.59$ and clutch size: $\chi^2 = 0.03$, df = 1, $P = 0.87$). There was no difference in age composition between responding and non-responding groups: 51 yearlings and 10 older individuals in the hissing group and 36 yearlings and 6 older individuals in the non-hissing group, respectively (Fisher's exact test: P = 0.98).

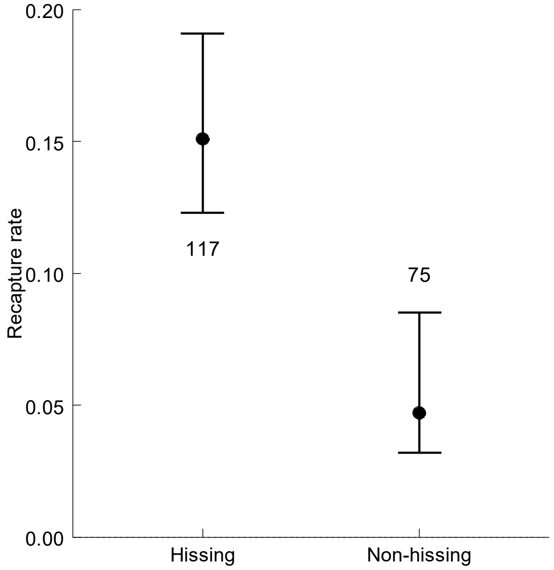

Figure 2. Recapture rate of the ringed individuals in the following year among the hissing and non-hissing females. Whiskers denote standard errors.

3.3. Habitat preference and population density of hissing and non-hissing birds (II, III)

A link was observed between hissing behavioural type and population density along the transects of the next-boxes. Great tits that elicited hissing display tended to breed in locations with decreased nest-box occupancy (P = 0.028) and bred further away from the closest occupied nest-box (P = 0.05) when compared to the non-responding individuals (**II**).

The proportion of hissing great tits was higher in coniferous forests (71%) when compared to deciduous (54%) (**III**).

3.4. Predation risk and hissing behaviour (II)

I examined nest depredation rates in association with the hissing response types over three years (2011–2013). All occurrences of nest predation events throughout the first nesting period (from the beginning of incubation until fledgling stage) were registered. Predation risk was separately calculated in each transect as the ratio of failed nests (both depredated and deserted combined) to occupied nest-boxes. The type of hissing response from female great tits was not related to nest predation risk (**II**).

3.5. Association of hissing behaviour with polymorphisms in two candidate genes (IV)

Two candidate genes were tested for association with hissing or non-hissing response types; the dopamine receptor gene D4 (*DRD4*; the SNP830) and the serotonin transporter gene (*SERT*; all the SNPs in exonic regions and the promoter region were studied). SNP830 in the *DRD4* gene had no effect on whether a female hissed or not (**IV**). The SNP187 in SERT gene exon 1 correlated significantly with female behavioural response (**IV**). Pairwise post-hoc tests showed significant difference between AT and TT genotypes of the SNP187, while not between AA and TT genotypes, probably due to the very small sample size of the AA genotype (**IV**). TT homozygotes tended to display hissing whereas the heterozygotes and AA homozygotes stayed silent.

4. DISCUSSION

4.1. The variability and the repeatability of the hissing behavioural types

This study confirmed that the hissing response of individual female great tits during incubation remained variable, and at the same time stayed individually consistent over time (**I**, **II**, **III**). My results showed that on average, 62% of females reacted towards a woodpecker model during the first 5 seconds and the rest remained silent (**III**). In comparison, Møller *et al.* (2021) and Riyahi *et al.* (2022) have reported smaller percentages (27% and 44%, respectively) of hissing great tit females in their study population. It may be of importance that in the former study, an instant response type to a sudden disturbance was registered by removing the lid of the nest-box, whereas in the second study, a mouse model was presented through the nest-hole and the number of hisses were counted during a 15-second trial. Despite methodological differences, if a larger dataset was available, it would be interesting to compare whether different populations along the north-south gradient, or in the relationship between human-related disturbance levels (urban *versus* rural) create a difference between the proportions of hissing and non-hissing individuals. Differences in the nest defence (the hissing propensity in my study) between populations may be derived from differences in the average stress level of individuals in each habitat (Réale *et al.* 2010, Geffroy *et al.* 2020). Hence, it may be that hissing is more common in regions with higher risk of nest predation, presumably in northern latitudes when compared with southern populations, or in rural areas with large forests, farther from human activity.

According to my hypothesis, I found that the hissing type of response was highly repeatable in great tits when measured several days later (**II**) and moderately repeatable over substantial parts of the lifespan (**III**) and did not change with age. This is consistent with Møller *et al.* (2021), who reported that female great tits in northern Denmark maintained the same hissing type when tested multiple times in the same breeding season. Hence, I suggest that the propensity to hiss during the incubation stage is a relatively consistent behavioural trait within populations and very likely involves some information about individual behavioural phenotype. In line with these findings, studies on different vertebrate animals have shown that different individuals are predisposed to respond differently to the same predator under similar conditions (Smith 1991, Eilam *et al.* 1999). It has been shown that several anti-predator behaviours such as flight initiation distance in birds (Carrete and Tella 2010, Evans *et al.* 2010, Seltmann *et al.* 2012) and lizards (Carter *et al.* 2010) or distinctive freeze and flee responses in a swift species (Bize *et al.* 2012), are heritable and consistent across the lifetime. It seems that individual variation in behavioural strategies might be explained by aspects of neuroendocrinology, and especially by differences in hormone levels. For example, voles that fled in response to owl calls exhibited higher levels of stress-induced corticosterone and they were more active before the exposure to the predator than those that froze (Eilam *et al.* 1999), or another example, owl nestlings that hissed more intensely also had a lower breathing rate under stress and were more docile when handled indicating to lower corticosterone response (van den Brink *et al.* 2012).

4.2. The hissing behaviour and reproductive performance

The hissing or non-hissing response types did not relate to early reproductive investment (lay-date, clutch size) or body condition (**II**, **III**). Parental investment theory is based on the establishment that parents adjust their anti-predator behaviour according to the value of their brood (Rytkönen 2002). For example, it has been demonstrated experimentally in the pied flycatcher (*Ficedula hypoleuca*) that parents reduce risk-taking when the number of nestlings has been reduced (Tilgar and Kikas 2009). However, the studying of the hissing response during the incubation period hopefully targeted the essence of the behaviour on an individual level, that was detached from the soliciting behaviour of the brood. Presumably, the reproductive investment in eggs did not not explain behavioural differences between hissing response types. Interestingly, Thys *et al.* (2019) reported that more fiercely hissing females laid smaller clutches. The discrepancy between the studies may be explained by population-specific differences in the selection pressure, operating on anti-predator behaviours (Biro and Stamps 2008, Réale *et al.* 2010). Or alternatively, it may be related to the specific trait that was measured (hissing intensity as a continuous trait used by Thys *et al.* (2019) *versus* hissing type as a categorical trait in my study).

I also found that heavier females (weighed at the fledgling state) initiated egg-laying earlier in the season among non-hissing birds, but this was not the case among the hissing group (**II**). This possibly indicates that non-hissing females may represent a heterogeneous group of birds in terms of parental quality. Some of them (late breeders) were more affected by seasonal constraints influencing the late breeding conditions than hissing individuals. This can be explained by the low quality of these birds on one hand, or on the other, that they lost more body mass during the breeding period due to the increased provisioning of the brood. Hence, the variation in phenotypic quality among different behavioural groups might be revealed in a very different way. I suggest for example that female parental quality among hissing birds might be better reflected by the intensity of the response, as illustrated by Thys *et al.* (2019). It may also be that the type of hissing response type alone does not carry information about individual quality. This emphasises the complexity of individual fitness and the need to be cautious when evaluating individual quality.

Although hissing behaviour was not related with females' reproductive potential in investing in eggs, I found that non-hissing females were significantly more successful at raising eggs to fledglings than hissing ones (**III**). Several mechanisms might explain the difference in breeding success between the two distinct groups. **First**, the behavioural phenotype of the birds of the non-hissing group somehow led to better parental abilities. Presumably, non-hissing birds represent the reactive phenotype. Perhaps such individuals are slow but thorough explorers, and that it may be an advantage when seeking food for the offspring. Although the question about behavioural flexibility in relation to the hissing type was not addressed in my study, it is possible that non-hissing birds adjust their behaviour more according to the situation, somehow resulting in better parental care. Hence, non-hissing birds may be more successful in finding food in a fluctuating environment. As a result, they might be more successful at raising neonates to fledglings when compared to hissing birds. Similarly, Both *et al.* (2005) reported that slow-exploring female great tits had fledglings in better condition in early nests, but this effect disappeared later in the season. In agreement with this hypothesis, I cannot exclude the possibility that the non-hissing birds that bred in the late season lost more body mass when compared to hissing birds because they provided higher level of parental care under poor environmental conditions (**II**). **Second**, active predator avoidance may be related to other predator-related activities, making the birds of the hissing type allocate more time to anti-predator behaviours, resulting in poor parental care (Duckworth 2006, Hollander *et al.* 2008). Hence, I may speculate that due to the trade-off between different activities, hissing birds probably devoted less time to brooding or feeding the chicks. **Third**, it is possible that hissing calls were uttered by impulsive but shy individuals (Riyahi *et al.* 2022). If hissing birds are more anxious and more sensitive to potential predators, they may be spending more time off from the nest after a disturbance or be less willing to feed the young under a risky situation. If so, the nests of the hissing birds were more likely to suffer brood reduction as those parents were more engaged with activities related to self-defence rather than nest-defence. **Fourth,** I suggest that variation in hissing behaviour might be reflective of different life-history strategies. Life-history theory suggests that individual lifetime fitness consists of different components that can be prioritized differently at an individual level (Réale *et al.* 2010). I found that recapture rates were higher for the responding phenotype, nevertheless, breeding success from eggs to fledglings was remarkably higher for non-responding birds. Hissing birds may have invested less in current reproduction than non-hissing birds and therefore the residual reproductive component that was related to higher survival probabilities was increased. Thus, and unexpectedly, the enhanced anti-predator behaviour (active hissing) of great tits was negatively related to a fast pace of life. At first glance, this is counter-intuitive as the commonly held understanding is that boldness-like behaviours, such as hissing display, are positively related to fast life-histories and high investment in reproduction (David and Dall 2016). That is, when hissing is reflective of boldness (see also Thys *et al.* 2021). However, the relationship between reproduction and behavioural strategies can vary intra-specifically because different behavioural phenotypes may prioritise different fitness components. Alternatively, the benefits and costs of different strategies vary in different contexts and environments

(Adriaenssens and Johnsson 2009; Nicolaus *et al.* 2016). Previous studies on great tits have consistently reported negative (Both *et al.* 2005), positive (Vrublevska *et al.* 2015) or no association (Hollander *et al.* 2008) of exploratory behaviour with fledgling success.

4.3. Associations of the hissing behaviour with predation risk, population density, and habitat preference

The probability of nest depredation during the breeding cycle did not relate to the hissing type of the birds living in the survey area (**II**). At first it appears that this result is inconsistent with previous studies, suggesting that anti-predator behaviours may be enhanced in risky environments (Lima 2009, Krams *et al.* 2010). It has been documented previously that the probability of nest predation is positively associated to predator abundance (Angelstam 1986, Andren 1992). However, several studies have demonstrated that the hissing sounds of great tits may deter the potential nest predators (Zub *et al.* 2017, see also the experiment with feral cats in the Latvian population in Paper I). In another example, Zanette *et al.* (2011) manipulated the abundance of predators in a wild population of song sparrows (*Melospiza melodia*) and found that the perception of perceived predation risk was itself powerful enough to affect prey behaviour and population dynamics. However, the missing link between predation risk and the hissing type of the females in my study may be related to the rather small differences in predation risk between territories and habitats and may not contribute significantly to the variation of hissing responses. Alternatively, as hissing behaviour was found to be a repeatable trait, environmental factors such as variation in depredation risk may have had little or no effect on the behavioural response in the short term (within the same breeding season), whereas the risk level can shape this trait over a longer timescale. In agreement, Zhang *et al.* (2020) reported no connection between hissing behaviour and predation risk within the same nesting population of five different tit species. Notably, among responding females, hissing delay was non-linearly related to lay-date, possibly following seasonal changes in the probability of nest predation. Hence, I cannot exclude that seasonal variation in predation risk may have some effect on the hissing propensity, at least at a local scale.

Hissing females tended to nest in transects of lower conspecific abundance and breed in nest-boxes further away from the closest occupied nest-box (**II**). One explanation could be that hissing birds may have been more aggressive toward conspecifics, resulting in bigger territories. Female great tits are known to defend the area close to the nest, and even a little further (Slagsvold 1993), suggesting that hissing females might be behaving more dominantly or aggressively towards conspecifics, driving the neighbours farther away, leading to larger territories and lower densities (see also Mougeot *et al.* 2003). Furthermore, if hissing reflects a female's aggressiveness, such birds might form a breeding pair with more aggressive males through assortative mating (Both *et al.* 2005). As the great tit is a territorial species, aggressive individuals may hold larger territories, resulting in a low population density around hissing females. Hissing great tits might drive neighbours further away by acting fiercely and unpredictably. But in a recent study (Thys *et al.* 2021) no link between hissing and aggressiveness was found. So, alternatively, hissing birds may be avoiding interspecific connections due to higher sensitivity towards conflicts, for example. In a group-forming spider, *Anelosimus studiosus*, who displays distinctive behavioural phenotypes, either aggressive or docile, when multiple individuals were placed in forced groups in the laboratory, the more aggressive individuals preferred to position themselves further away from the conspecifics (overview given by Grinsted and Bacon 2014). The latter assumption was also supported by the observation that females were more likely to hiss in coniferous rather than in deciduous forests (**III**). In this context it should be remembered that the population density of great tits in deciduous habitat is about double that in coniferous forests (Mänd *et al.* 2005). It seems that benefits and costs of such behaviour may to some extent depend on extrinsic factors, such as resource availability, predator abundance or population density. However, whether this spatial variation in hissing behaviour is adaptive or not, remains unclear.

4.4. Polymorphisms in two candidate genes in association with hissing response types

It has been proposed that individual differences in response to stressors are mediated via dopaminergic and serotonergic neurotransmission systems (Turner *et al.* 2017). In my study population of great tits, a link was found between the genotype and the type of response behaviour (hissing or non-hissing) towards a nest intruder (**IV**). More specifically, I found that the hissing response in great tits can be associated with single nucleotide polymorphism in the SERT gene (SNP187 in exon 1), but not to the DRD4 gene. TT genotype displayed an active acoustic defence towards an intruder, while AT heterozygotes and AA homozygotes remained silent and passive. This polymorphism is synonymous and does not lead to a change in the protein sequence. However, non-synonymous and synonymous SNPs have similar probability for gene–behaviour associations in humans (Sauna and Kimchi-Safaty 2011) and birds (Holtmann *et al.* 2016, Müller *et al.* 2014). These effects may affect mRNA structure, the rate of translation or post-translational modifications of polypeptides (Nackley *et al.* 2006). In the SERT gene, the polymorphism may act as a transcriptional enhancer (Fiskerstrand *et al.* 1999). It is likely that complex behavioural traits are influenced by a number of interacting genes suggesting that clearly more studies are needed to understand the effect of SNPs on behavioural responses. Indeed, a recent study by Riyahi *et al.* (2022) found a significant association between SNP290 in the SERT promoter and hissing response of great tits. Taking all of this together, despite the lacking mechanisms, these different studies indicate the crucial role of SERT gene polymorphism in adjusting anti-predator behaviours of great tits.

5. CONCLUSIONS

My results indicate that the hissing response type has a genetic background, and the population mean values vary slightly with extrinsic factors such as habitat type and breeding density. The results suggest that life history trade-offs observed during the four-year study are the result of differences in decision-making rather than differences of phenotypic quality or age-related experience. Presumably, the reaction type exhibited by female great tits might, for example, be better explained by genetic variation between individuals, making the hissing response a useful measure when positioning individuals along the slow–fast axis of a behavioural phenotype. From an evolutionary perspective, individual differences in the hissing response may have co-varied with proxies for fitness such as survival and reproductive success. It seems that the negative association between breeding success and recapture rates in my study population partially explained the co-existence of these distinct anti-predator responses. I conclude that hissing could be a suitable trait for investigating differences in behavioural strategies, leading to differences in fitness.

6. SUMMARY

Investigating personality in animals and its consequences to life-history has become great interest of animal ecologists and conservation biologists. Nevertheless, measuring personality and defining its characteristic in animals is difficult. It seems to be especially important to study naturally relevant behaviours, like anti-predator behaviour as it is one of the greatest aspects affecting individual fitness. In the current study, anti-predator behaviour in the great tit (*Parus major*) was determined as hissing or not towards a sudden threat. The behavioural test to determine the differences between individual females was designed to mimic a predator entering the entrance of the nest-hole, blocking the incubating bird to initiate escape, and therefore enforcing the female to use the hissing behaviour as a likely measurement of nest-defence. However, the hissing response as a behavioural reaction is not only common to incubating females but also males, and even other species across taxa. Over 4 years I collected data about great tits' hissing behaviour and breeding characteristics, hoping to reveal a possible pattern that might help to assess the variability and consistency of this trait as well as to explain the co-existence of hissing and non-hissing birds in a wild population. I hypothesised that 1) differences in hissing behaviour are consistent both within season and across seasons, 2) hissing behaviour may be influenced by early reproductive value, 3) hissing may be enhanced under some environmental indices, 4) hissing and non-hissing birds differ genetically.

My findings demonstrated that the hissing response of an individual bird was repeatable within and over different breeding seasons. There was no habituating to the predator model between repeated trials. The response was either elicited fast (during the first 5 seconds) or not at all, with a few exceptions of females initiating hissing display later. Each year, the proportion of hissing females remained larger when compared to non-hissing birds. Hissing response was unrelated to nest predation risk. Interestingly, hissing birds tended to breed in areas of lower conspecific abundance and were more likely found nesting in coniferous than deciduous forests. Start of egg-laying, clutch size and hatching success did not predict hissing response type. However, I found that non-hissing females of great tits were more successful at raising eggs to fledglings, revealing a fitness consequence of the hissing behavioural phenotype. Moreover, recapture rate across the years was higher in the hissing females compared to the non-hissing group of birds. Additionally, I found that hissing and non-hissing females had different genotypes; the mutation in the single nucleotide was found in the serotonin transporter gene. TT genotype in the exon 1 of the SERT gene displayed the active hissing response while AT heterozygotes and AA homozygotes remained silent and passive.

The results presented in this thesis suggest that variation in hissing behaviour may be related with different life-history strategies and might be attributed to personality in great tits along the slow-fast continuum. I suggest that hissing or not hissing in a threatening situation carries some information about the behavioural phenotype of great tit females, reflected by parental abilities or survival. In conclusion, hissing behavioural type is a useful and informative personality-related trait to be measured on free-living female great tits.

7. SUMMARY IN ESTONIAN

Sisisev hoiatushäälitsus peegeldab emastel rasvatihastel (*Parus major*) käitumuslikku fenotüüpi ning sigimisedukust looduslikus populatsioonis

Loomad teevad otsuseid tulenevalt oma iseloomust ja igasugused otsused mõjutavad isendi kohasust. Seetõttu saab öelda, et iseloomutunnused on loodusliku valiku all, sarnaselt teistele fenotüübitunnustele. Loomaökoloogid ja looduskaitsebioloogid on hakanud suurt rõhku pöörama loomade käitumusliku varieeruvuse uurimisele. Peamised eesmärgid on välja selgitada käitumuslikku varieeruvust põhjustavad mehhanismid ning taolise varieeruvuse mõju erinevatele elukäigutunnustele. Sellest hoolimata, et iseloomu uurimine pälvib aina enam tähelepanu, valitseb jätkuvalt segadus uuringumetoodikas. Põhjuseks on asjaolu, et loomade iseloomu on keeruline nii hinnata kui ka defineerida. Tunnustatud arusaama järgi saab mingit käitumuslikku omadust iseloomuga seostada, kui see vastab järgmistele kriteeriumidele: 1) tunnust iseloomustab populatsioonisisene varieeruvus, 2) tunnus on korduv ajas ning eri kontekstides, 3) esineb tunnuse geneetiline pärandumine vanematelt järglastele. Valdavalt on levinud iseloomutunnuste hindamisel kahemõõtmeline skaala, näiteks kirjeldatakse käitumist kui reaktiivset või proaktiivset ning kiiret või aeglast. Samas on mitmed tunnused omavahel sageli seotud nii, et kujuneb niinimetatud käitumissündroom. Näiteks, kui isendit iseloomustab agressiivsus mingis olukorras, siis sellised isendid võivad suhelda ühtviisi agressiivselt nii liigikaaslaste kui kiskjatega. Iseloomutunnuste hindamisel tuleb esmalt hoolega läbi mõelda, millised käitumuslikud tunnused üldse iseloomu kirjeldamiseks sobivad. Hea oleks käitumist hinnata erinevates olukordades ning lisaks määrata ka füsioloogilisi näitajaid, et paremini mõista, kuidas erinevad tunnused omavahel seotud on ja kuidas mõjutavad tervikuna looma elukäiku. Väga oluline on arvesse võtta, et looma käitumine võib erineda vastavalt sellele, kas seda on mõõdetud laboritingimustes või loomulikus elukeskkonnas. Käitumise uurimine laboris võimaldab küll vältida segavaid tegureid, näiteks kisklust või partneri mõju, ent vangistuses mõõdetud käitumine ei pruugi anda ökoloogiliselt olulisi vastuseid. Siinkohal on huvitav välja tuua, et kui näiteks loomi püütakse loodusest, et seejärel nende käitumist laboris uurida, võib juhtuda, et saadakse kätte sarnase iseloomuga isendeid, kes mingil põhjusel paremini lõksu jäävad. Praeguseks on juba tänuväärsel hulgal kirjeldusi, kuidas käitumine looduses korreleerub elukäigutunnustega, näiteks ellujäämisega.

Käitumine ohuolukorras, eelkõige kiskjaga kohtumisel, on üks olulisemaid aspekte, mis mõjutab otseselt isendi kohasust. On teada, et liigikaaslased reageerivad kiskjatele erinevalt. Sellega seoses on välja pakutud, et julgemad ja agressiivsemad isendid võiksid samal ajal ka rohkem panustada paljunemisse ning järglaste eest hoolitsemisse. Seega, ägedam reaktsioon kiskjale võiks peegeldada justkui kiiret elukäiku, millele on iseloomulik kõrgem sigivus, ent madalam eluiga. Peab arvestama, et vastust kiskjale võivad mõjutada veel mitmed tegurid, näiteks pesakonna väärtus (nn vanemliku investeeringu teooria) ja ka varasem kogemus kiskjatega või nende kohtamise tõenäosus keskkonnas. Levinud viis mõõtmaks individuaalset kisklusvastast käitumisstrateegiat looduses on hinnata kiskja vältimisega seotud tegevusi. Lindudel on selliseks käitumuslikuks tunnuseks näiteks isendi kaugus kiskjast lendu tõusmise hetkel ehk kaugus isendi ja teda ohustava kiskja vahel, mille korral lind tõuseb lendu. Antud tunnust on lihtsam mõõta avatud maastikul. Suluspesitsejate puhul on sellist tunnust raske määrata, kuna lind võib olla pesas varjul. Ent mitmetel õõnsustes pesitsevatel linnuliikidel on välja arenenud omapärane hoiatushäälitsus ootamatu ohu korral – nad sisisevad. Näiteks tihaseliikidel on kirjeldatud häälitsust, mis meenutab mao sisinat ja mida sageli saadavad ägedad tiivalöögid ja nokahoobid. Seni on arvatud, et taoline käitumine esineb pesa kaitsmise eesmärgil, kuid näiteks rasvatihasel (*Parus major*) sisisevad mõlemad sugupooled ja sisisemist esineb ka väljaspool sigimishooaega. Lisaks on teada, et kõik isendid ei pruugi sisiseda. Minu töö eesmärk oli kirjeldada sisisemise kui iseloomuliku hoiatushäälitsuse esinemist rasvatihaste looduslikus populatsioonis ning leida võimalikke seoseid lindude elukäigutunnustega. Minu hüpoteesid olid järgmised: 1) sisisemine või selle reaktsiooni puudumine on individuaalsel tasandil ajas püsiv tunnus, mis isendite vahel populatsioonis varieerub, 2) sisisemine on seotud sigimispanuse ning oodatava elueaga, 3) sisisemise osakaalu populatsioonis võivad mõjutada keskkonnategurid, näiteks kiskjate arvukus või populatsioonitihedus, 4) sisisejad ja mittesisisejad erinevad üksteisest geneetiliselt, mis väljendub kahe kandidaatgeeni (dopamiini retseptori geen, *DRD4* ja serotoniini transporteri geen, *SERT*) polümorfismides.

Uurisin emaste rasvatihaste vastust pesa rüüstavale kiskjale nelja aasta vältel. Sisisemiskäitumise hindamiseks viisin käitumiskatse läbi pesitsusperioodi alguses, mil emaslinnud mune haudusid. Läbi pesakasti ava eksponeerisin hauduvale linnule 5 sekundi jooksul suur-kirjurähni (*Dendrocopus major*) topist. Jagasin linnud vastavalt nende reaktsioonile sisisejateks ja mittesisisejateks. Uurimistulemused näitasid, et igal aastal oli populatsioonis ligikaudu kolmandik selliseid emaslinde, kes ei sisisenud kiskja peale. Hoiatushäälitsuse kasutamine sama isendi poolt ühe pesitsushooaja vältel oli kõrge korduvusega tunnus, mis tähendab, et isendi käitumine ajas ei muutunud oluliselt. Lisaks õnnestus määrata väikese hulga lindude vastust kiskjale erinevatel aastatel ning ka sellisel juhul oli tegemist korduva tunnusega. Emase mass, munemisaja algus ning kurna suurus ei seostunud sisisemiskäitumisega. Oluline erinevus ilmnes aga poegade ellujäämuses: mittesisisejatel lennuvõimestus rohkem poegi kui sisisejatel. Seejuures munade koorumise edukus ei erinenud. Samal ajal selgus, et võrreldes mittesisisejatega võis sisisevate emaste ellujäämistõenäosus olla kõrgem, kuna nelja aasta jooksul taas tabatud emastest enamus olid sisisejad. Huvitaval kombel pesitsesid sisisevad emased tõenäolisemalt hõredamalt asustatud aladel ning lisaks ka keskmiselt kaugemal lähimast naabrist. Sisisejad pesitsesid sagedamini okasmetsas kui lehtmetsas. Sisisemisvastus pesitsusalal ei olnud seotud pesade rüüstamise tõenäosusega. Geeniuuringust selgus, et sisisejad ja mittesisisejad erinevad üksteisest ka genotüübi poolest: polümorfism *SERT* geeni eksonis 1 seostus emaslinnu hoiatushäälitsusega.

Minu töö põhjal võib järeldada, et tihastele loomupäraselt omane sisisemisreaktsioon iseloomustab emase rasvatihase käitumuslikku fenotüüpi. See, kas isend sisiseb või mitte, ei ole seotud tema panusega pesakonna suurusesse ega sõltu otseselt välistest teguritest, nagu näiteks kiskjate arvukus, mistõttu on alust arvata, et tegemist on geneetiliselt päritava tunnusega. Seda kinnitab ka leitud erisus erineva käitumistüübiga isendite genotüüpide võrdlemisel. Hoiatushäälitsuse esinemine võib peegeldada emastel rasvatihastel vanemliku hoole kvaliteeti, mis väljendub poegade lennuvõimestumise edukuses. Arvatavalt on põhjuseks üldisem iseloom, mille poolest sisisejad ja mittesisisejad erinevad, ning mis tingib ka erinevused nende käitumises. Näiteks võivad sisisejad panustada rohkem kiskjate tõrjumisele, jättes munad või pojad hooletusse, mille tulemusena väheneb pesakonnas lennuvõimestuvate poegade arv. Lisaks on võimalik, et sisisejad ja mittesisisejad valivad pesapaika erinevalt või mõjutavad erinevalt liigikaaslaste paiknemist populatsioonisisese suhtluse kaudu. Kokkuvõttes võib öelda, et sisisemiskäitumise abil on võimalik iseloomustada vabalt elavate rasvatihaste käitumuslikku fenotüüpi ja ennustada selle alusel isendi elukäigustrateegiat.

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